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A new species of *Amoria* (Gastropoda, Volutidae, Amoriinae) from the mid-east coast of Australia

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ABSTRACT

A new species of *Amoria* Gray, 1855 (Gastropoda, Volutidae) is described from shells dredged off the Australian mid-east coast (Cape Moreton, Queensland and Tweed Heads, New South Wales). *Amoria thorae* sp. nov. shows a number of similarities in shell form and/or colour pattern to two other small *Amoria*, *A. necopinata* Darragh, 1983 and *A. benthalis* McMichael, 1964 and to the much larger *A. undulata* (Lamarck, 1804) but can be readily distinguished from these and all other members of the genus by the combination of small shell size, fusiform shape, high spire, equal-sized thick columellar plaits and a single, large undulation of the axial lines.

❑ *Amoria, Volutidae, systematics, new species, eastern Australia.*

In their monograph of the genus *Amoria* Gray, 1855, Bail, Limpus & Poppe (2001) included a small unnamed species ('*Amoria* (*Amoria*) sp.') dredged off Cape Moreton (south-east Queensland) and off Wooli (northern New South Wales) and known only from two specimens held in private collections. Limpus (1996) had previously reported on the Wooli specimen, referring to it as '*Amoria* cf *necopinata*' and noting that it had been 'trawled in 125+ metres'. Bail *et al*., (2001) also pointed out similarities to *A. necopinata* Darragh, 1983, a Capricorn Channel and southern Swains species, and to the more widely distributed, but much larger and chiefly southern Australian species *A. undulata* (Lamarck, 1804) but, due to a lack of specimens, refrained from naming the species. Neither Bail *et al*. (2001) nor Limpus (1996) made any comparison with *A. benthalis* McMichael, 1964, which partly resembles the unnamed species and has a similar geographic range. When photographing the Thora Whitehead shell collection prior to its acquisition by the Queensland Museum, the author located two specimens of the unnamed species (labelled as *A. necopinata*), and subsequent searching by Alison Miller (Australian Museum, Sydney) produced two further shells (also labelled as *A. necopinata*). In this paper I take the opportunity to name the species in honour of Thora Whitehead, who has, for over 50 years, made a major contribution to Australian malacology.

MATERIAL AND METHODS

Specimens used in the description derive from the molluscan collections of the Australian Museum and the Queensland Museum (those from the latter, originally from the Thora Whitehead Collection, Brisbane). For comparison with other species of *Amoria*, shells of *Amoria necopinata* Darragh, 1983, *A. benthalis* McMichael, 1964 and *A. undulata*

(Lamarck, 1804) from these collections and from the Thora Whitehead Collection were also examined. Shell measurements were made using Vernier callipers, with precision of 0.1 mm. The deep-focus images of the holotype (Fig. 1) and paratype 3 (Fig. 4A) were focus-stacked with Zerene Stacker software from source images taken with a Canon 5DS camera on a Dun Inc. BK-Plus imaging system. Specimens shown in Figs 3-4 were photographed using a Panasonic Lumix DFC-MZ8 camera with a Leica optical zoom lens and built-in flash. Specimens shown in Fig. 6 were photographed using a Nikon D810 camera with a 70 mm Sigma Art macro lens with studio flash.

ABBREVIATIONS

AMC, Australian Museum molluscs collection (Sydney, New South Wales); NSW New South Wales; QLD, Queensland; RC, Reserve Collection (dry shell collection); SA, South Australia; SE South-east; VIC, Victoria; QMMO, Queensland Museum molluscan collection (Brisbane, Queensland).

SYSTEMATICS

Class GASTROPODA Cuvier, 1795

Order NEOGASTROPODA Wenz, 1938

Family VOLUTIDAE Rafinesque, 1815

Subfamily AMORIINAE Gray, 1857

Genus *Amoria Gray, 1855*

Type species. *Voluta turneri* Gray (= Gray in Griffith & Pidgeon, 1834) (by subsequent designation, Harris (1897)).

Amoria thorae sp. nov.
(Figs 1, 2, 3, 4, 5A, E, 6A-D)

Amoria cf *necopinata* Darragh, 1983. Limpus (1996), pp 1 & 3.
Amoria (*Amoria*) sp. Bail, Limpus & Poppe (2001), p. 45, Pl 56, Figs 1,2; pl 84; pl 85, Fig.2

Material examined. HOLOTYPE: AMC.75849, (RC) dredged off Cape Moreton, QLD (no depth recorded) 27° 2'S, 153° 36'E, 1970, presenter O. Rippingale. PARATYPES: QMMO.85858, (paratype 1), RC, 1, trawled at 110 m off Cape Moreton, SE QLD, (no date recorded), presenter T. Whitehead. QMMO.85859, (paratype 2), RC, 1, same data as paratype 1. AMC.364620, RC, 1, (paratype 3), #9056B, off Tweed Heads, NSW 28° 14' – 28° 19'S, 153° 50'E , depth 128-137 m, by FRV "Kapala", 2 June, 1978. Station: K78-09-09/10. Collector: K.J. Graham, ex AMC.114257. *Amoria thorae* sp. nov. LSID reference urn:lsid:zoobank.org:act:9741B918-3092-4D8F-B855-204EE11C4E64

Etymology. Named for Thora Whitehead for her many years of dedication to the study of molluscs and for her generous assistance to numerous individuals and societies throughout the world malacological community.

Diagnosis. The combination of small shell size and fusiform shape, high spire, equal-sized, thick columellar plaits and a colour pattern dominated by a single large undulation of the axial lines (overlying four rows of diffuse brown blotches) distinguishes this species from all other *Amoria* spp.

Description. Shell small for *Amoria* (adults 24.8-31.6 mm total length), moderately solid, narrow, high-spired and fusiform. Aside from growth lines, sculpture lacking and surface smooth. Protoconch conical of about two and a half whorls but transition to teleoconch very subtle; nucleus almost flat. Teleoconch of two to two and a half whorls; body whorl weakly concave toward suture, strongly convex at shoulder and very slightly convex to almost straight thereafter; suture impressed; aperture long and narrow; columella slightly curved, bearing four thick equal-sized plaits, the posterior two sometimes associated with low, weakly-developed secondary plaits; outer lip curved and solid, thickest posteriorly; anterior fasciole raised and well-defined; siphonal notch well-developed; anal notch moderately well-developed. Protoconch colour cream. Teleoconch base colour cream to tan, with overlying parallel, brown, axial lines; body whorl with 14-25 (average 18) axial lines which show one undulation peak directed towards the aperture (when viewed dorsally); underlying the axial lines of body whorl are four indistinct rows of light brown blotches, one row below the suture, two mid-whorl (best developed) and one close to anterior fasciole;

TABLE 1. Dimensions of the type series.

Specimen designation	Registration Number	Shell length	Length of aperture	Maximum shell width
Holotype	AMC.75849	24.8 mm	17.8 mm	10.9 mm
Paratype 1	QMMO.85858	27.8 mm	20.7 mm	12.4 mm
Paratype 2	QMMO.85859	24.3 mm	17.8 mm	10.4 mm
Paratype 3	AMC.364620	31.6 mm	22.7 mm	13.6 mm

fasciole with 5-8 axial lines. Animal presently unknown.

Distribution. Cape Moreton, SE QLD to Wooli, northern NSW (approximately 300 km); known bathymetric range 110-137 m (dead shells only) (see Fig. 2).

Habitat. Unknown.

Comments on the type series. Of the four specimens comprising the type series of *A. thorae* sp. nov. (all dead-taken shells), the holotype, a small adult, is the most structurally intact and although somewhat faded still retains most of the colour pattern (Figs 1, 3A, E, 5A, E, 6A). Paratype 1, a slightly damaged adult with partial apertural encrusting by serpulid polychaetes, best shows the intensity of the colour pattern (Figs 3B, F, 4B, C, 6B). Paratype 2 is a juvenile, very damaged on the apertural side (Figs 3C, G, 4C, 6C), and paratype 3, a faded and partially bryozoan-encrusted adult but with the best preserved protoconch, is the largest of the series and also the largest known specimen (Figs 3D, H, 4A,C, 6D). Secondary columellar plaits (weakly-developed) are only evident in the holotype and paratype 1 (Fig. 4B). The marked difference in size between the holotype and paratype 3, both conchologically 'mature' specimens, raises the possibility of sexual dimorphism in the species, although this can only be determined once mature living animals - and statistically-analysable numbers of them - are found. Predation drill holes, likely of muricid and octopodan origin, are present in the three paratypes (paratype 1 - one on protoconch, one near anterior extremity of fasciole; paratype 2 - one on protoconch, one on early teleloconch; paratype 3 - one on protoconch) (Fig. 4C).

Comparison with other species of *Amoria*

Amoria thorae sp. nov. can be compared with several other *Amoria* spp. with axially-lined shells (see Plate 84 of Bail *et al.*, 2001), but three stand out as showing the strongest conchological similarities: *A. necopinata* Darragh, 1983, *A. benthalis* McMichael, 1964 and *A. undulata* (Lamarck, 1804) (see Figs 5, 6 for comparative photographs). The following summarises the principal differences of these three species from *A. thorae* sp. nov.

Amoria necopinata (Figs 5B, F; 6E-J) differs from *A. thorae* sp. nov. in having: a thinner shell; a more expansive, convex aperture; thinner, more widely spaced columellar plaits; a deeper anal notch; an ivory-white shell background with a colour pattern devoid of underlying blotches and featuring fewer axial lines on the body whorl (13-14) – the lines forming two undulation peaks. Additionally, a brown spiral line is usually visible, running around the suture between the last protoconch whorl and first teleoconch whorl. The anterior fasciole has only one to three axial lines.

Amoria benthalis (Figs 5C, G; 6K-O) differs from *A. thorae* sp. nov. in having: a broader and generally larger shell; a noticeably shorter spire; a larger, broader protoconch, often with a distinct glaze; larger columellar plaits (the posterior being largest); a weakly defined anterior fasciole; a deeper anal notch; a colour pattern featuring a greater number of axial lines on the body whorl (25-32) – the lines showing either two or no undulation peaks.

Amoria undulata (Figs 5D, H; 6P-T) differs from *A. thorae* sp. nov. in having: a much larger shell (typically 60-80 mm); a larger, broader protoconch of 3 ½ -4 whorls; a deeper

FIG. 1. Holotype of *Amoria thorae* sp. nov. AMC.75849, dredged off Cape Moreton, SE QLD; **A,** Dorsal view; **B**, Ventral (apertural) view; **C**, Lateral view; **D**, View looking down on spire showing detail of protoconch.

anal notch; a colour pattern in which the axial lines usually exhibit two or more undulation peaks. Juveniles of *A. undulata* of the same size range as *A. thorae* sp. nov. are, by comparison with the new species, stocky with a wide, distinctly angulate shoulder (Fig. 6 P-T).

Two other species of *Amoria* whose geographic ranges partially overlap that of *A. thorae* sp. nov. are *A. zebra* (Leach, 1814) (Northern New South Wales to Northern Queensland, an exclusively shallow water species) and *A. canaliculata* (McCoy, 1869) (Cape Moreton to Swain Reefs, Queensland). These species very occasionally fall into the shell-size range of *A. thorae* sp. nov., but neither could be confused with it (*A. zebra*: pupiform protoconch, shell very thick and broad, shorter spire, very thick columellar plaits, no axial line undulation; *A. canaliculata*: shell very thick and broad, shorter and deeply channelled spire, very thick columellar plaits, no axial line undulation) (see Abbotsmith 1969; Weaver & DuPont 1970; Poppe & Goto 1992; Wilson 1994; Bail *et al*. 2001).

All other species of *Amoria* with axially-lined shells have geographic ranges far removed from that of *A. thorae* sp. nov. and can be readily distinguished from it on shell features: *A. ellioti* (G.B. Sowerby II, 1864) (Western Australia), *A. jamrachi* Gray, 1864 (Western Australia), *A. turneri* (Gray in Griffith & Pidgeon 1834) (Western Australia to Torres Strait, Queensland) (all with much larger shells, shorter spires, axial line undulation peaks either absent or irregular), *A. macandrewi* (G.B. Sowerby III, 1887) (Western Australia) (larger shell, shorter spire, with 2-3 axial line undulation peaks), *A. dampieria* Weaver, 1960 (Western Australia) (shell small but very thick, with shorter spire, very thick columellar plaits, no axial line undulations) (see Abbotsmith 1969; Weaver & DuPont 1970; Poppe & Goto 1992; Wilson 1994; Bail *et al*. 2001). The Timor subspecies of *A. grayi*, *A. grayi kawamurai* Habe, 1975, does show a single large undulation peak of the body whorl axial lines but this peak, when viewed dorsally, faces the opposite direction to that of *A. thorae* sp. nov., and the shell is much larger and its facies show an obvious, strong affinity with Western Australian *Amoria* (see Poppe & Goto 1992; Wilson 1994; Bail *et al*. 2001).

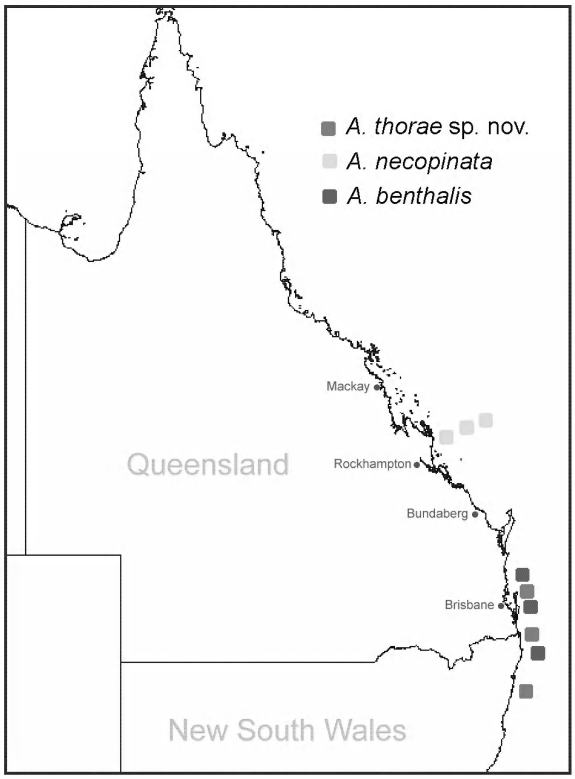

FIG. 2. Map contrasting known distributions of *Amoria thorae* sp. nov., *A. necopinata* Darragh, 1983 and *A. benthalis* McMichael, 1964.

Other Remarks. Although the holotype and paratypes of *Amoria thorae* sp. nov. are dead-taken specimens, they clearly belong to the same species illustrated by Bail *et al*., (2001) as '*Amoria* (*Amoria*) species' (their plate 56, figures 1 and 2: likewise a dead-taken specimen, albeit in fresher condition that the type series of *A. thorae* sp. nov.). The two specimens examined by Bail *et al*. (2001) were trawled off Cape Moreton (southern Queensland) and off Wooli (northern New South Wales – their illustrated specimen). Locality data for the type series of *A. thorae* sp. nov. not only confirm that the species occurs off Cape Moreton but importantly, with the existence of a Tweed Heads shell (paratype 3), help to bridge an apparent gap between Cape Moreton and Wooli, thereby giving a known

FIG. 3. Type series of *Amoria thorae* sp. nov. from dorsal view (A-D) and ventral/apertural view (E-H). **A, E,** holotype, AMC.75849, dredged off Cape Moreton, SE QLD; **B, F,** Paratype 1, QMMO.85858 110 m trawled off Cape Moreton, SE QLD; **C, G,** Paratype 2 (QMMO.85859; same data as Paratype 1); **D, H,** Paratype 3, AMC.364620, #9056B, 128-137 m off Tweed Heads, NSW.

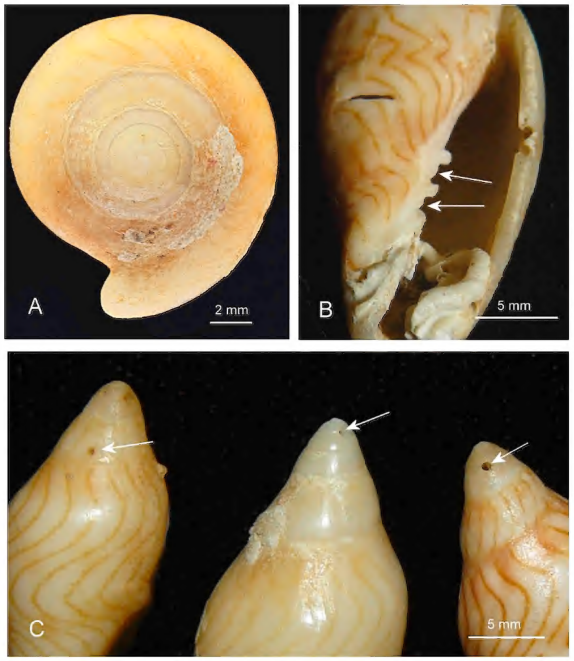

FIG. 4. *Amoria thorae* sp. nov. **A**, View looking down on spire showing detail of protoconch of paratype 3 (AMC.364620). **B**, Apertural view of paratype 1 (QMMO.85858) showing weakly developed secondary plates (arrows) between primary plates. **C**, Predation drill holes (arrows) in paratypes (left to right) paratype 2 (QMMO.85859, likely octopodan drill hole), paratype 3 (AMC.364620, likely muricid drill hole), paratype 1 (QMMO.85858, possible muricid drill hole).

FIG. 5. *Amoria thorae* sp. nov. (**A, E,** holotype, AMC.75849, dredged off Cape Moreton, SE QLD) contrasted (from both dorsal and apertural perspective showing columellar plaits) with *A. necopinata* Darragh, 1983 (**B, F,** AMC.101845. 133.5 m, Capricorn Channel, off North Reef Lighthouse, Coral Sea, QLD), *A. benthalis* McMichael, 1964 (**C, G,** QMMO.83608, 170 m, off Moreton Island, SE QLD) and a typical juvenile *A. undulata* (Lamarck, 1804) (**D, H,** QMMO.30632, Hawks Nest, SA).

range of approximately 300 km for the species. This range substantially overlies that of *A. benthalis* (Mooloolaba, southern Queensland to Ballina, New South Wales) (see Fig 2) although, as the present paper has shown, that species can readily be differentiated on shell features from *A. thorae* sp. nov. Hopefully further collecting will determine the depth at which living *A. thorae* sp. nov. may be found. Possibly it is deeper than the recorded maximum for the type series (137 m) as extensive shallow-water (<100 m) trawling throughout the known range over many years by fishing vessels has not produced specimens, at least to the author's knowledge. Given that the terrain worked by commercial trawlers is of necessity (e.g. safety, potential damage to boat and gear – see Evans, 2000) very select, it is also possible that the new species lives near areas avoided by boats, such as coarse rubble and/or rocky reefs, but within the known bathymetric range, or shallower. However, Alison Miller (Australian Museum, Malacology Department) was able to supply the author with a list of 29 other molluscs species (5 bivalves, 24 gastropods) dredged together with paratype 3 of *A. thorae* sp. nov. from off Tweed Heads, New South Wales. Most if not all of these are associated with mud, sand or shell grit bottoms, and all four of the other volute species present (*Athleta studeri* (Von Martens, 1897), *Ericusa sericata* Thornley, 1951, *Cymbiolacca complexa* Iredale, 1924, *Nannamoria parabola* Garrard, 1960) live either on mud and/or sand (Coleman 1975; Poppe & Goto

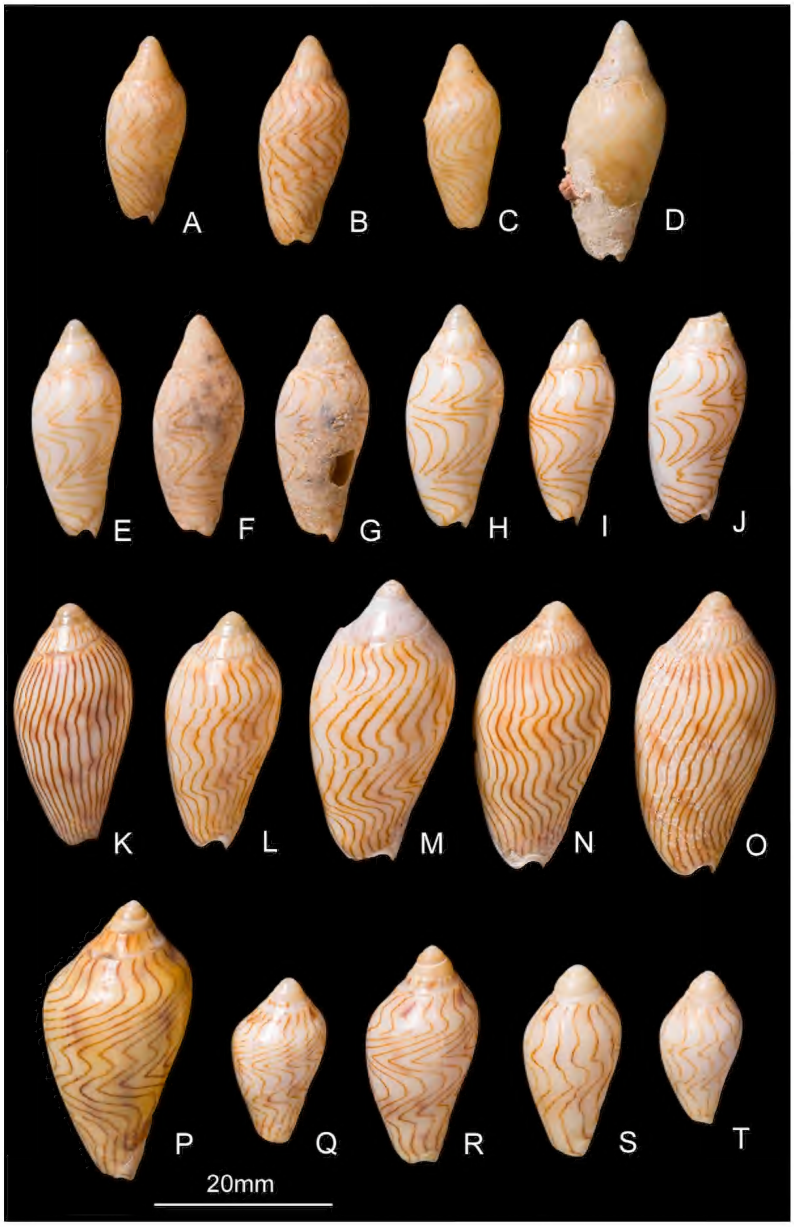

FIG. 6. Comparison of shell series of *Amoria thorae* sp. nov. with similar species of *Amoria*, showing general consistency of shape and colour pattern within each species. **A-D**. *Amoria thorae* sp. nov; **A,** Holotype (AMC.75849, Cape Moreton, SE QLD); **B, C,** Paratypes 1 (QMMO.85858) and 2 (QMMO.85859), both 110 m, off Cape Moreton, SE QLD. **D,** Paratype 3 (AMC.364620, 128-137 m off Tweed Heads, NE New South Wales); **E-J,** *A. necopinata* Darragh, 1983; **E-G,** AMC.101845, 133.5 m, Capricorn Channel, off North Reef Lighthouse, Coral Sea, QLD; **H, I,** QMMO.85878, Coral Sea, QLD; **J,** QMMO.83660, 140 m, Capricorn Channel, Coral Sea, QLD; **K-O,** *A. benthalis* McMichael, 1964; **K,** QMMO.63431, off Cape Moreton, SE QLD. **L, M,** QMMO.83608, 170 m, off Moreton Island, SE QLD; **N, O,** QMMO.85879, 200 m off Mooloolaba, SE QLD; **P-T,** Juvenile *A. undulata* (Lamarck, 1804); **P, Q,** QMMO.25166, Sorrento, VIC; **R,** QMMO.30632, Hawks Nest, SA; **S, T,** QMMO.85880, Eastern Cove, Kangaroo Is, SA).

1992; Bail & Limpus 2015.). The three species here considered closest to *A. thorae* sp. nov. (*A. necopinata*, *A. benthalis*, *A. undulata*) are also associated with mud and/or sand (see Weaver & Dupont 1970; Poppe & Goto 1992; Limpus 1993; Bail *et al*. 2001), and on balance, such a substratum seems likely for the new species. Given the small shell size of *A. thorae* sp. nov., and the fact that modern trawling methods are designed to exclude unwanted benthic by-catch, locating living specimens may prove difficult, particularly if the species is genuinely uncommon or rare. The fact that all known specimens of *A. thorae* sp. nov. are dead-taken should not be misconstrued as evidence that the species is actually extinct (i.e. that the known shells are 'sub-fossils'). For example, the vast majority of *A. necopinata* and *A. benthalis* encountered are dead-taken shells (Coucom 1975a, b; Bail *et al*. 2001; Evans 2001), yet both species are unquestionably living ones as documented in colour photographs of the animals (Coucom 1975b; Bail *et al*. 2001; Healy 2015).

Concerning the precise relationship of *A. thorae* sp. nov. to other *Amoria* species, little can be said with any certainty until animals are available for study. Conchologically, the new species would appear to have closest connections with the similarly small-sized *A. necopinata* and *A. benthalis* and with the much larger and more widely distributed *A. undulata.* Bail *et al*. (2001), in their comments on *A. necopinata* (p. 34), hinted that the two specimens observed by them of '*Amoria* (*Amoria*) species' (= *A. thorae* sp. nov.) may actually be variants of *A. necopinata*, but later in the same study (p. 44) suggested that the same specimens may be closer to *A. undulata* based on range and colour pattern. The known distribution of *A. necopinata* is well separated from even the most northerly record of *A. thorae* sp. nov. (Fig. 2) and despite similarities in shell size and shape and a shared tendency towards possession of secondary columellar plaits, the two taxa are readily distinguished on other shell features. As also shown in this paper, *A. thorae* sp. nov. cannot be confused with *A. benthalis* nor with *A. undulata* of the same shell size (the latter specimens invariably being juvenile, broad-shouldered and angulate). Importantly, the known geographic range of *A. thorae* sp. nov. overlaps that of *A. benthalis* and the northern-most east coast limit of *A. undulata* (see Abbotsmith 1969; Bail *et al*. 2001) indicating that the new species is not an ecophenotype of either of these taxa. Indeed, judging from available bathymetric data, all three of these species could potentially be sympatric. Published photographs of living *A. necopinata*, *A. benthalis* and *A. undulata* (Coucom 1975b; Coleman 1975; Wilson 1994; Bail *et al*. 2001; Healy 2015) may provide clues as to the appearance of the animal of *A. thorae* sp. nov. Both *A. necopinata* and *A. benthalis* show alternating yellow/white and brown/orange transverse bands on the tentacles and reticulate markings on the siphon, whereas in *A. undulata* the tentacles and siphon are both longitudinally striped. Such information, aside from helping to confirm that *A. benthalis* is a valid species (and not, as suggested by Darragh (1983, 1988) an end-of-range dwarf form of *A. undulata*), also provides an anatomical link between *A. necopinata* and *A. benthalis*. It will be of interest to know if the markings of the cephalic tentacles and siphon of *A. thorae* sp. nov. are like those of *A. necopinata* and *A. benthalis*, or like those of *A. undulata*, or perhaps follow some other scheme. As *A. necopinata*, *A. benthalis*, and *A. undulata* all exhibit reticulate brown markings on the foot (contrasting with the radiating stripes of the foot seen in most other *Amoria* spp. – Weaver & DuPont 1970; Wilson 1994; Bail *et al*. 2001), it is likely that *A. thorae* sp. nov. also shares this feature. Finally, an examination of the radulae of *A. thorae* sp. nov., *A. necopinata* and *A. benthalis* is here considered important to confirm that these species possess the 'typical' *Amoria* Y-shaped rachidian teeth seen in *A. undulata* (see McMichael 1964).

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and juvenile *A. undulata* for comparisons. Alison Miller of the Australian Museum (Malacology Department) is thanked for her considerable help in locating, within that institution's extensive collection, additional specimens of *A. thorae* sp. nov. (which have become the holotype and paratype 3) as well as material of *A. necopinata* and *A. undulata* for comparisons and for the list of other molluscs collected with paratype 3 by the "Kapala" (Ken Graham) from off Tweed Heads. Dr Mandy Reid (Collections Manager, Malacology Department, Australian Museum) kindly allowed me the opportunity to examine the Australian Museum material. Geoff Thompson (Collections Imager, Queensland Museum) took the high definition (image-stacked) photographs of the holotype (Fig. 1) and protoconch of paratype 3 (Fig. 4A); Peter Waddington (Photography, Queensland Museum) photographed specimens for Fig 6; all other photographs (Figs 3, 4B, C, 5) are by the author. Thanks are also due to Sarah Verschoore (Biodiversity and Geosciences Program, Queensland Museum) for her assistance with the map (Fig. 2) and the referees for their very helpful suggestions on the manuscript.

LITERATURE CITED

Abbotsmith, F. 1969. *Multiform Australian Volutes.* (Privately published) 108pp + later addenda.

Bail, P. & Limpus, A. 2015. The eastern Australian *Cymbiola* Swainson, 1831. New revision of the subgenus *Cymbiolacca* Iredale, 1929. The "pulchra complex" 1998 updated. *Visaya Supplement* **6** (Conchology Inc., Lapu-Lapu City) 95pp.

Bail, P., Limpus, A & Poppe, G. 2001. *A Conchological Iconography. The Genus Amoria.* (ConchBooks, Hackenheim), 50 pp, 92 pls.

Coleman, N. 1975. *What Shell Is That ?* (Hamlyn, Sydney) 308pp.

Coucom, C. 1975*A*. To be – or not to be. *Keppel Bay Tidings* **14**(2): 1 & 4.

1975b. Capricorn Channel volutes. *Keppel Bay Tidings* **14**(4): 1, 4 & 5.

Darragh, T.A. 1983. Volutidae (Mollusca: Gastropoda) from the Capricorn Channel, Central Queensland, Australia. *Journal of the Malacological Society of Australia* **6**(1-2): 83-87. https://doi.org/10.1080/00852988.1983.10673959.

1988. A revision of the Tertiary Volutidae (Mollusca: Gastropoda) of south-eastern Australia. *Memoirs of the Museum of Victoria* **49**(2): 195-307. https://doi.org/10.24199/j.mmv.1988.49.12.

Evans, R. 2000. Prawn trawling off the Sunshine Coast. The 60's & 70's. Part 1 (The grounds… deep and shallow and their shells). *Keppel Bay Tidings* **39**(1): 7.

2001. Prawn trawling off the Sunshine Coast, the 60's and 70's (The winter months …70-105 fathom deep-water grounds). *Keppel Bay Tidings* **40**(1) : 6-7.

Harris, G.F. 1897. *Catalogue of Tertiary Mollusca in the Department of Geology, British Museum (Natural History). Part I. The Australasian Tertiary Mollusca.* (British Museum [Natural History], London).

Healy, J.M. 2015. Colour images of deep water *Volutidae. Radula* (Spring): 3.

Limpus, A. 1993. *Amoria necopinata* Darragh, 1983. A welcome visitor. *Keppel Bay Tidings* **32**(2): 1 & 5.

1996. To be – or not to be. *Keppel Bay Tidings* **35**(3): 1 & 3.

McMichael, D. 1964. Notes on the genera *Amoria* Gray, 1855, and *Zebramoria* Iredale, 1924, (Gastropoda: Volutidae), with descriptions of new species. *Records of the Australian Museum* **26**(8): 265-274. https://doi.org/10.3853/j.0067-1975.26.1964.676.

Poppe, G.T. & Goto, Y. 1992. *Volutes.* (L'Informatore Piceno, Ancona), 348pp.

Weaver, C.S. & DuPont, J. 1970. *The Living Volutes.* (Delaware Museum, Greenville), i-xv + 375pp.

Wilson, B.R. 1994. *Australian Marine Shells. Prosobranch Gastropods. 2 (Neogastropoda).* (Odyssey Publishing: Kallaroo), 370pp.

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Probable predation of the semi-aquatic Rusty Monitor Lizard (*Varanus semiremex*) by a Groper

Predation of varanids (Monitor lizards) is limited to some degree due to many large species being apex predators or placed high in the food chain. Juveniles or smaller species of monitors, the latter often referred to as Pygmy Monitors in Australia, are far more susceptible to predation and succumb to a range of predators. Snakes, larger lizards, birds of prey and carnivorous mammals are known to prey on smaller varanids (Pianka *et al.* 2004). Not surprisingly, the author was unable to find any reference to predation of a monitor by a fish; hence, the following documented observation of a Queensland Groper regurgitating a Rusty Monitor is of some significance.

The Rusty Monitor (*Varanus semiremex*) is a semi-aquatic species of monitor lizard endemic to Queensland and restricted to coastal mangroves. Until recently, little had been documented about its natural behaviour in the wild. While information on husbandry (Jackson 2005), feeding behaviour, home range and longevity (Tremul 2017) has been published, the only predation records are inferred from their behaviour in response to the presence of Coastal Carpet Pythons and birds of prey (Tremul 2017). Here I present new data on the probable predation of a Rusty Monitor by a fish.

On the 17th of January 2017 at 11:40 am, Kurt Emmerton was fishing for Mangrove Jack in Monte Christo Creek (adjacent to Curtis Island) when he caught a juvenile Queensland Groper in approximately 3 metres of water. Once the fish was netted he realized that it had what appeared to him to be a 'crocodile-like' creature in its mouth. Both fish and reptile were lifted into the boat, placed on the floor and quickly photographed before releasing the fish and discarding its prey (Fig. 1.). The fish was confirmed by Jeff Johnson, Ichthyologist, at the Queensland Museum as a Queensland Groper (*Epinephelus lanceolatus*) I identified the lizard as a Rusty Monitor (*Varanus semiremex*), based on dorsal pattern, size and head scalation.

Estimated measurements of goanna and fish by use of scale in Fig.1 are 50-52 cm and 42-45 cm respectively. Cogger (2014) lists the Rusty Monitor as having a total length of 60 cm. Hence the Rusty Monitor regurgitated in figure 1 was of adult size, whilst the Queensland Groper, a large fish measuring up to 2.7 metres long, was a juvenile (J. Johnson, pers. comm.).

FIG. 1. Queensland Groper with a regurgitated Rusty Monitor. Image provided by Kurt Emmerton.

The Rusty Monitor is well known as an inhabitant of tidal mangrove swamps along the east coast of Queensland (Wilson & Swan 2013; Cogger 2014) and I have observed individuals swimming between partially submerged trees on numerous occasions (Tremul 2017). This behaviour would potentially place the species as vulnerable to predation by large surface feeding fish.

The Queensland Groper is a formidable, opportunistic predator and is likely to take advantage of an opportunity to prey on a monitor swimming above, particularly in a shallow water situation (Jeff Johnson, pers. comm.).

The Rusty Monitor in this observation was probably swimming when eaten, rather than being picked up as floating carrion; the overall body condition and marks where the flesh has been torn are consistent with a recent kill. The bite radius and its position on one side of the lizard's body are typical of damage caused by a fish of this size (Jeff Johnson; pers. com).

Based on the photographic evidence, there is no indication to suggest that the monitor was mauled or gnawed earlier or that it had been dead for any period of time. Although it is not possible to determine where the monitor was eaten, the groper's capture site was surrounded by mangrove habitat that is suitable for Rusty Monitors. Hence the author believes that the Queensland Groper, along with other large carnivorous surface-feeding fish inhabiting estuaries, is a predator of the Rusty Monitor. A direct observation of this type of predation is unlikely to occur as Rusty Monitors are cryptic in behaviour and the fish would snatch its prey quickly from the surface. Perhaps this explains why there are currently no records of a Rusty Monitor engaging in underwater feeding behaviour.

Observations of swimming behaviour (Tremul 2017) show that Rusty Monitors swim directly to an exit point. A swimming monitor holds its head clearly above water in a position allowing it to have good vision of its surroundings but leaving it exposed to attacks from below. By reducing its time spent in the water, a monitor decreases its vulnerability to aquatic predators, an understandable tactic in light of the present observation.

ACKNOWLEDGEMENTS

The author sincerely thanks Kurt Emmerton for sharing his thorough knowledge on fishing and generously permitting use of the image displayed in Figure 1. Andrew Amey gave editorial advice and provided a sounding block for my ideas; his willingness in helping a field naturalist publish work is greatly appreciated. Jeff Johnson kindly provided information on the feeding behaviour and identification of a Queensland Groper. Patrick Couper's encouragement and advice on animal ethics is always welcome. My wife Inge is very supportive of my work and the time spent achieving it. Thanks also to the two reviewers, whose comments greatly assisted in improving the original draft.

LITERATURE CITED

Cogger, H.G. 2014. *Reptiles and Amphibians of Australia.* (CSIRO Publishing: Collingwood).

Jackson, R. 2005. The poorly known Rusty Monitor *Varanus semiremex*: History, Natural History, Captive Breeding and Husbandry. *Herpetofauna* **35**(1): 15-24.

Pianka, E.R., King, D.R. & King, R.A. (2004) *Varanoid Lizards of the World.* (Indiana University Press: Bloomington).

Tremul, P.R. 2017. Field observations provide an insight into the ecology of the Rusty Monitor (*Varanus semiremex*) in South-eastern Queensland, Australia. *Memoirs of the Queensland Museum – Nature* **60**: 77-89. https://doi.org/10.1082/j.2204-1478.60.2017.2016-05.

Wilson, S. & Swan, G. 2013. *A Complete Guide to Reptiles of Australia*. (New Holland Publishers Pty. Ltd: Australia).

TREMUL, P.R. Honorary Officer, Queensland Museum, PO Box 3300, Qld 4101. Accepted: 23 July 2019. Published online: 31 January 2020.
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Revision of *Cerabilia* Laporte, 1867 (Carabidae: Abacetini) of Australia and New Caledonia

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ABSTRACT

Cerabilia Laporte, 1867 of Australia and New Caledonia are revised. *Biliacera, a* new subgenus is described for the New Caledonian species. 50 species are newly described bringing the total for the genus to 61 species. From Queensland, Australia 26 species are described in the subgenus *Feronista* Moore, 1965: *Cerabilia (Feronista) australiensis* sp. nov., *C. (F.) bellensis* sp. nov. *C. (F.) blatta* sp. nov., *C. (F.) danbullaensis* sp. nov., *C. (F.) gigas* sp. nov., *C. (F.) haigensis* sp. nov., *C. (F.) iridescens* sp. nov., *C. (F.) kalkajaka* sp. nov., *C. (F.) lewisensis* sp. nov., *C. (F.) loxandroides* sp. nov., *C. (F.) montivaga* sp. nov., *C. (F.) moorei* sp. nov., *C. (F.) mudda* sp. nov., *C. (F.) oodiformis* sp. nov., *C. (F.) parva* sp. nov., *C. (F.) prolixa* sp. nov., *C. (F.) prosopogmoides* sp. nov., *C. (F.) reflexa* sp. nov., *C. (F.) securilata* sp. nov., *C. (F.) spinifer* sp. nov., *C. (F.) spuh* sp. nov., *C. (F.) storeyi* sp. nov., *C. (F.) stylata* sp. nov., *C. (F.) tipica* sp. nov., *C. (F.) uncata* sp. nov., *and C. (F.) wunduensis* sp. nov. The four existing species of *Feronista* are also redescribed. From New Caledonia 24 *Biliacera* species are described: *Cerabilia Biliacera aite* sp. nov., *C. (B.) amieuensis* sp. nov., *C. (B.) apicesecta* sp. nov., *C. (B.) discosetosa* sp. nov., *C. (B.) dominatrix* sp. nov., *C. (B.) drupa* sp. nov., *C. (B.) edentata* sp. nov., *C. (B.) espee* sp. nov., *C. (B.) francisca* sp. nov., *C. (B.) inversa* sp. nov., *C. (B.) kanakorum* sp. nov., *C. (B.) klingonorum* sp. nov., *C. (B.) koghisensis* sp. nov., *C. (B.) letalis* sp. nov., *C. (B.) mouensis* sp. nov., *C. (B.) nana* sp. nov., *C. (B.) neocaledonica* sp. nov., *C. (B.) orbiculata* sp. nov., *C. (B.) paniensis sp. nov., C. (B.) rubrica* sp. nov., *C. (B.) ruginosa* sp. nov., *C. (B.) sternovillosa* sp. nov., *C. (B.) vitalis* sp. nov., *and C. (B.) wisei* sp. nov. A key to adult beetles of all species, distributional maps, illustrations of the male genitalia, the pronota, and other diagnostic features are provided. Images of all holotype specimens and their labels are provided in an appendix.

❒ *Loxandrina, Rainforest beetles, inverted aedeagus, Queensland endemic beetles*

The genus *Cerabilia* was described in 1867 by Laporte (using one of his pseudonyms, Compte de Castelnau) for *C. maori* from New Zealand. Subsequently, Broun, over several papers, described the bulk of the New Zealand species in the genus *Zabronothus* Broun, 1893. These two genera were brought into synonymy by Larochelle and Larivière (2007). Up to 2011 all the New Zealand *Cerabilia* were classified in Platynini (Will 2011; Larochelle & Larivière 2016). This traditional placement was based on the lack of the elytral plica and general facies that is similar to some sphodrines such as members of *Calathus* Bonelli, 1810, or perhaps a stout form of Platynini. That *Cerabilia* might have been misplaced, was brought to my attention in 2008 (J.K. Liebherr pers. comm.) and, study of several New Zealand species clarified that they should be included in Abacetini (Will 2011, 2015). Moore (1965) described the genus *Feronista* for three Australian rainforest species that also share the characteristic form

and absence of the plica. Moore placed these in Pterostichitae and in his informal "abacetine series." The final species described prior to this contribution was *C. monteithi* (Baehr 2007), which was mistakenly placed in Masoreini based on the lack of the plica, spiny tibiae and relatively long metatibial spurs. Small-sized *Cerabilia*, like Baehr's species, can easily be mistaken for a masoreine or perigonine. Given the frequent absence of the elytral plica in abacetines (Straneo 1991) caution and detailed examination is required to appropriately place these taxa.

Examination of the male genitalia and female reproductive tract, together with features of the external morphology (Will 2011, 2015) and DNA data (Will unpublished) confirm that Moore's placement in Abacetini is correct and within the tribe, *Cerabilia* is placed in Loxandrina Erwin and Sims, 1984. Additionally *Cerabilia* and *Feronista* are closely related with the genus previously reported to occur in New Caledonia (Will 2011). The species listed here are newly described.

This contribution only treats species from Australia and New Caledonia. At the present time there is insufficient material available to revise the New Zealand taxa. Among the handful of specimens from there that I have examined, there appeared to be many individuals that do not fit the original descriptions of the seven species currently recognised, suggesting there is a significant undescribed diversity. Additionally, the morphological character states among the handful of New Zealand taxa that I have examined do not resolve the relationship of these species relative to the Australian and New Caledonian species. Evidence does support the Australian and New Caledonian taxa as reciprocally monophyletic. It is for convenience and as a working-hypothesis, that the New Zealand species are placed with the type species for the genus in *Cerabilia* sensu stricto. It is possible that they form a grade rather than a monophyletic group, but testing this remains to be done and will be part of a future phylogenetic analysis.

Specimens of Australian and New Caledonian *Cerabilia* have been collected in wet forests and rainforests, typically in leaf litter. A few specimens were taken using pyrethrum spray of tree trunks and logs. The most consistent method of collection, and the means by which the largest series have been collected, is to search and rake leaf litter at night. These flightless beetles appear to be hypogeal during the day and are found rarely under woody debris, rocks, or other large surface cover—situations where one typically would look for Carabidae. I have observed beetles in Australia and New Caledonia emerging from the cracks and small burrows in the soil after full-dark arrives. Specimens taken on trunks and logs using pyrethrum spray were cases of extreme wet, where beetles are probably moving up to avoid water-saturated soils. Pitfall traps also are somewhat effective in collecting specimens of *Cerabilia*, though usually not large numbers of any one species. My observations suggest that the nocturnal, epigeal activity of the beetles is limited and patchy and so the opportunity for beetles to enter traps is limited.

Despite the challenge of acquiring specimens of *Cerabilia*, a sufficient number have been collected and studied to make a substantial advance in the understanding of the diversity of the group. While the Queensland fauna has been reasonably well sampled, primarily through the efforts of Geoff Monteith (QM), the fauna of New Caledonia is probably still tremendously under-sampled, particularly in the North Province. Given the current reality and future threat of habitat modification and loss due to humans modifying habitats and the changing climate, it is critical to discover and describe baseline biodiversity. This contribution is a small step in that grand effort.

The male genitalia and female reproductive tracts are significantly diverse among *Cerabilia* species. In comparison to related abacetines, e.g., *Loxandrus* LeConte, 1853 and *Pediomorphus* Chaudoir, 1878, the diversity of forms and differences between species is much greater. The general body form among species of *Cerabilia* does not vary as widely, all are flightless, convex, and have a very compact thorax (Figs

1–9). However, in addition to the remarkable variation of reproductive structures, there are a number of external morphological characters— typically stable in most groups— that vary among the species of *Cerabilia*. For example, the presence or absence of setae on the elytral disc and pronotal lateral margins, the presence, size, and setae of mentum pits, presence and absence of the mentum tooth, and the development of tarsal sulci, all vary. The extent of variation may be due to the antiquity of the genus, a distinct possibility given its distribution, or more recent, relatively rapid diversification.

MATERIAL AND METHODS

Material examined. A total of 275 specimens of *Cerabilia* were examined from the following collections: ANIC- Australian National Insect Collection, Canberra; CAS- California Academy of Sciences, San Francisco; EMEC- Essig Museum of Entomology, Berkeley, California; MNHN- Museum National d'Histoire Naturelle, Paris; NMHW- Naturhistorisches Museum, Wien; NZAC- New Zealand Arthropod Collection, Auckland; QM- Queensland Museum, Brisbane; QDAF- Queensland Department of Agriculture and Fisheries, Brisbane. For species described herein, all specimens examined are listed under the type material. For previously described species, type material information is listed and any additional specimens examined are reported in a section following the redescription.

Specimen deposition. Holotypes are deposited per instructions from all pertinent collecting permits issued to K.W.Will, information received from collectors regarding their permits, and explicit instructions from source institutions. Recent material from New Caledonia is covered by permits that require holotypes be lodged in MNHN, Paris. These list the place for deposition and also credit the source institution as they have borne all the costs facilitating loans, curating, and maintaining specimens.

Label information. Locality information for holotype specimens of species described here are presented verbatim. Text as it appears on the labels is contained in quotation marks. The text for each label is delimited by double forward slash marks. For specimens other than the holotypes of newly described species the presented label information is normalised and condensed. Specimens bearing tags with "EMEC####" have these unique identification numbers for data entered in the publically available Essig database (essigdb.berkeley.edu) and do not represent the specimen deposition or ownership. Label text in the form of "KWW###" represents gDNA sample vouchers held at UC, Berkeley. Type localities are based on the holotype labels and clarified and described in more detail where possible. Images of all holotypes, dorsal and left lateral views, and labels, for all species treated here are included in Appendix A, available as an online supplement.

Dissection methods. For routine morphological study, the female reproductive tracts and the male aedeagus samples were cleared using a pancreatin solution (Alvarez-Padilla & Hormiga, 2007 (2008)), held in a warming oven at 37° C overnight or in a 10% KOH solution, warmed on a hotplate. For samples that were used to generate gDNA samples (Will unpublished) from soft tissue, digestion was done with proteinase-K using the standard methods for the DNeasy Tissue Kit® (Qiagen, Valencia, CA). Dissections digested in KOH were neutralised in 10% acetic acid, and those treated with pancreatin and proteinase-K were washed in distilled water. Median lobes were then moved to glycerin for study and storage. Female reproductive tracts were stained in chlorazol black and processed using the same methods as used by Liebherr and Will (1998) and then stored in glycerin.

Measurements. External structures were examined using a dissecting stereo-microscope at magnification of 100x or less. Measurement were made using an ocular reticle in a stereomicroscope. Standard body length (SBL) is the sum of the distance from the base of the labrum to just anterior of the occipital suture + the length of the pronotum along its midline + the length of the left elytron from basal margin

where it meets the scutellum to the apex of the elytron. Generally SBL will be slightly greater than an apparent length, which is the whole length as viewed from above, due to the fact that the head and in some cases the pronotum, is flexed ventrally. The width of the elytra is the widest point viewed dorsally. The ocular ratio is the width over the eyes divided by the width between the eyes, measured at the level of the anterior supraocular setae, viewed dorsally.

Images. Pronotal, habitus, and other images were taken as digital image stacks that were aligned and assembled with Helicon Focus version 5.3. Composite image files were edited to enhance clarity and to digitally excise the pronotum using standard image editing software. Holotypes and their associated label images were taken as single images using a high-depth of field lens and were not edited further. Line drawings of the male genitalia and female reproductive tract were created by imaging the cleared and stained (staining only for females tracts) structures that were temporarily mounted in K-Y®, glycerin-based lubricant. These images were used as the basis for drawing the vector files.

Descriptions. Descriptions were initially generated using Lucid Builder, ver. 3.6. Features and states were scored in Lucid and a draft "natural language" description output from the program. This text was then edited for readability. Characteristics that are uniform at the genus and subgenus level are only included under those in the characteristics sections. Using Lucid generated descriptions has the advantage of producing complete and parallel descriptions, however they are more verbose than traditional descriptions. While any state that is uniform across all species in a genus-group is summarised under the higher taxon and not repeated, if even one species has an alternative state the feature must be included in all descriptions. In more tradition taxonomic works, such a feature might be discussed and variation noted in a summary elsewhere, perhaps under the genus, and then only the rare states explicitly described, requiring the reader to carefully intuit the states when not explicit.

Diagnoses and Identification. Characters given in the key and structures of the male genitalia can be used to differentiate all species treated here. When possible male genitalia should be used to confirm identifications. Differential diagnoses focus on distinguishing between similar species and, to avoid redundancy, typically do not refer to characteristics of the male genitalia or those covered in the key. Rather, diagnoses provide an additional set of attributes that can help with identification.

Terminology. Descriptions and keys used are standardardised from scientific literature and as defined in glossaries such as Torre-Bueno (1989). However, the complexity of the forms of ventral macrosculpture in *Cerabilia* requires the use of some particular, less familiar, terms. The surface of the ventral sclerites, particularly of the thorax, may be smooth or have various degrees of sculpturing that can vary in depth and regularity. The following terms: scabriculous- having a lightly impressed, rather irregular network or series of lines; rugulose- lines are deeper and more regularly parallel; rugose- still more deeply impressed in part, but varies in depth and is less regular in form; rugosissimus- very deep, dense, and parallel impressions, typically covering the entire sclerite when present.

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SYSTEMATICS

Abacetini Chaudoir, 1873
Loxandrina Erwin and Sims, 1984

Cerabilia Laporte, 1867: 116

Type species *Cerabilia maori* Laporte, 1867:116, by monotypy. Republished description Laporte, 1868:202.

= *Nelidus* Chaudoir, 1878: 49; type species *Nelidus australis* Chaudoir, 1878: 50, by monotypy. Synonymized by Will (2015).

= *Zabronothus* Broun, 1893: 1327; type species *Zabronothus striatulus* Broun, 1893:1327, designation by Larochelle & Larivière (2001). Synonymized by Larochelle and Larivière (2007).

= *Australomasoreus* Baehr, 2007: 6; type species *Australomasoreus monteithi* Baehr, 2007:6, by original designation. Synonymized by Will (2015).

Subgenus *Feronista* Moore, 1965: 25; type species *Feronista amaroides* Moore, 1965: 26, by original designation. Moved to *Cerabilia* by Will (2015).

Subgenus *Biliacera* Will, subgen. nov.; type species *Cerabilia vitalis* sp. nov.

Published references to the genus: Bowie, 2008b, 2008a; Guéorguiev & Sciaky, 2015; Liebherr & Will, 2015; Monteith, 2018; Moore *et al.*, 1987; Larochelle & Larivière, 2001, 2005, 2007, 2016; Lorenz, 2005a, 2005b, 2018; Will, 2011, 2015; Watts *et al.*, 2014.

Cerabilia sensu lato

Characteristics. Piceous or brown, rarely with paler markings on elytra, medium to small sized beetles. Range of 3.4–11.5 mm, greatest width over elytra 1.2–4.4 mm. Head with frontal impressions absent or at most represented by very shallow, ill-defined punctiform marks. Antennae: filiform, antennomere 1 with one large dorsal seta, antennomere 2 with ring of fine small setae at apex, antennomeres 5–11 pubescent except for medial glabrous strip on wide face. Clypeus with one pair of setae near anterior margin. Glossal sclerite with two large setae near apex on ventral side, paraglossal apices glabrous. Mentum shape clearly broader than long, moderately emarginate, sides of sinus divergent, lobes rather angular, with a single pair of fine setae paramedially near anterior margin. Suture between mentum and submentum present and clearly impressed. Maxilla with apical and medial setae of stipes absent, basal seta of stipes present, lacinia large with thick, curved apical digitus and medial field of spines and setae. Eyes relatively small or very small, flat or prominent. Pronotum with overall shape typically transverse, greatest width slightly to significantly greater than length. Flight wings absent. Elytra fused. Elytron with two setigerous punctures beyond umbilicate primary puncture near humeral angle in interval 9. Plica absent. Parascutellar setigerous punctures present at base of stria 2. Elytral parascutellar stria present, joined to stria 1. Angular base of stria 1 absent. Metepisternum form short, width of anterior margin about 2x lateral length. Legs rather stout and spinose. Metatrochanter seta present at basal third to near middle of length. Anterior tarsi of male with three basal segments obliquely dilatate and squamose beneath. Tarsal claws smooth. Abdominal sternites not sulcate. Ventrites III–V each with one pair paramedial setae. Aedeagus with parameres conchoid, the lower (in repose) smaller than the upper. Defensive gland reservoir shape simple ovoid.

Geographic Distribution. Northeastern Australia, New Caledonia, and New Zealand.

Subgenus *Cerabilia sensu stricto*

Characteristics. Preliminary character states presented here are modified from the description by Larochelle and Larivière (2007). As for the genus above, relatively robust (Fig. 1) with size range length 5.0–11.0 mm; body form stout, oblong. Eyes small, convex. Mentum with median tooth entire; paramedial pits small. Submentum with four setae. Pronotum very or moderately transverse, trapezoidal or rectangular; base wider than apex, or base and apex subequal in width; usually two (rarely one, anteriorly) setigerous punctures on each side. Prosternal process not margined. Protibiae with dorsal longitudinal grooves. Metatibiae curved. Tarsi glabrous dorsally; metatarsomere 5 glabrous ventrally; meso- and metatarsomeres 1 dorsally grooved, not carinate-sulcate. Shoulders broad, obtuse, with a prominent tooth. Parascutellar puncture absent. Elytral interval 3 with or without discal setigerous punctures. Umbilicate series with 15–18 setigerous punctures.

Geographic Distribution. New Zealand. The New Zealand species have not yet been studied in detail. As a working-hypothesis they are placed in *Cerabilia sensu stricto* as *incertae sedis*. It is possible that they form a grade rather than a monophyletic group relative to *Feronista* and *Biliacera*.

Included species: *Cerabilia maori* Laporte, 1867

Included *incertae sedis*: *Cerabilia aphela* (Broun, 1912); *Cerabilia major* (Broun, 1912); *Cerabilia oblonga* (Broun, 1910); *Cerabilia rufipes* (Broun, 1893); *Cerabilia striatula* (Broun, 1893); *Cerabilia australis* (Chaudoir, 1878).

Subgenus *Feronista Moore*, 1965: 25

Characteristics. As for the genus SBL range of 3.9–11.5 mm, greatest width over elytra 1.5–4.4 mm. Supra- and postorbital region smooth or with slight depressed areas around setae. Ocular ratio 1.09–1.47. Labral apical

margin with six setae. Mentum with paramedial pits deep, sharply defined, very small, diameter much less than 1/2 width between pits, paramedial pits glabrous. Maxillary antepenultimate palpomere glabrous or with 1–2 small apical setae, penultimate palpomere glabrous. Pronotum with margins bisetose, posterolateral setae present. Elytron interval 3 without setigerous punctures. Prosternum smooth. Proepisternum smooth. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Dorsal surface of meso- and metatarsomeres glabrous. Ventrites IV–VI glabrous. Pygidial gland secretions (known from two species (Will & Attygalle unpub. data)) consisting primarily of formic acid, which is mixed with smaller amounts of decane, undecane, 2-tridecanone, 2-pentadecanone, or 1-pentadecene.

Geographic Distribution. Found only in eastern Queensland, Australia (Figs 81–90).

SPECIES TREATMENTS

Cerabilia (Feronista) amaroides (Moore, 1965: 26)

(Figs 2, 29, 55, 77, 90)

Feronista amaroides Moore, 1965

Type material. HOLOTYPE, ♂. "S. QUEENSLAND: Gladstone district, Mt. Jacob [=Bulburin State Forest], c2000 feet, iii.58 (Darlingtons)". ANIC.

Specimens examined. Holotype and three additional males (QM) and two females (EMEC), all from type locality.

Diagnosis. Very distinctive large, broad and robustly built beetles (Fig. 2) with color and luster as in the smaller species, *C. (F.) mudda* below.

Redescription. *Size.* SBL 9.5–10.5 mm, greatest width over elytra 3.9–4.4 mm. *Head.* Dorsal microsculpture not apparent at 50x magnification. Eyes average size, convex. Ocular ratio 1.35. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt and triangular. Maxilla: apical palpomere glabrous or plurisetose with short, scattered setae, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 29): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle or ended well apicad hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals slightly convex in apical third, flat in basal third, widths all approximately equal, interval 9 with 17 or 18 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification or sculpticells transversely elongate, longitudinally short relative to body axis, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, very small, shallowly punctate. Prosternum rugose along apical margin. Metepisternum macrosculpture rugulose or lightly scabriculous. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally with fine, short, scattered setae, form

broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. Defensive gland chemical compounds from defensive glands formic acid, decane, undecane, 2-tridecanone, 2-pentadecanone or 1-pentadecene. *Male* genitalia (Fig. 55): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract (Fig. 77): apical margin of gonocoxite-1 glabrous, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa long, left directed curved form, common oviduct inserted near apex, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca short, width at middle 2/3 total length, spermatheca duct very short, about 2/3 length of reservoir, spermathecal gland duct connected at base of spermatheca, gland duct length very elongate, gland duct diameter increasing apically, without notable expansion, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) australiensis sp. nov.
(Figs 15, 70, 81)

Etymology. The specific epithet *australiensis* is based on the Australian provenance of these beetles and it is treated as an adjective.

Type material. HOLOTYPE, ♀. "Cardwell Range, N.E. QLD. Mt Macalister, 900 m 18–20 Dec 1986 Monteith, Thompson & Hamlet, Pitfall traps"//"QM Reg. No. T20037"//"EMEC1012229". Deposited QM. PARATYPE. Cardwell Range, Upper Broadwater Ck. Valley 17–21 Dec 1986, 700–800 m. G.B. Monteith, G. Thompson, Hamlet, Pitfall traps, QM Reg. No. T20036, EMEC1012230, ♀, QM.

Type locality. Queensland, Mt. Macalister. Estimated coordinates: 18° 18'S 145° 56'E.

Diagnosis. The notably emarginate basal margin, narrower form, and obtusely angled hind angles of the pronotum (Fig. 15) distinguish this species from *C. (F.) iridescens* and other similar species.

Description. *Size.* SBL 4.3–4.7 mm, greatest width over elytra 2.1(-2.2) mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.24. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 15): microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins convergent in basal half, lateral marginal bead well defined from apical angle ended well apicad hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture

smooth, microsculpture not apparent at 50x magnification, luster moderately glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form longer than half femur length, acuminate to rounded point. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire. Male genitalia: male unknown. Female genitalia and reproductive tract (Fig. 70): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa right side significantly longer than left, overall relatively stout, cup-shaped, right lateral portion of bursa with relatively short pouch, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) bellensis sp. nov.
(Figs 39, 64, 78, 83)

Etymology. The specific epithet *bellensis* is based on the type locality Bell Peak and is treated as an adjective.

Type material. HOLOTYPE, ♂. "AUST: QLD: NE: Graham Range, 9 Apr 1979, G.B.Monteith, QM BERLESATE NO. 4, 17.17S 145.57E, Rainforest, 100–200 m"//"QM Reg. No. T20038"//"EMEC1012233". Deposited QM. PARATYPES. North Bell Peak, via Gordonvale, 16 Sept 1981 G.Monteith & D.Cook, Q.M. Berlesate No. 300 Rainforest, 900–1000 m Sieved Litter and Moss, QM Reg. No. T19992, EMEC1012181, same with QM Reg. No. T19991, EMEC1012180; QM Reg. No. T19990, EMEC1012179 and QM Reg. No. T19989, EMEC1012178, 4♀♀, QM. North Bell Peak, 22 Nov 1990, G.Monteith & G.Thompson, Q.M. Berlesate No. 845, Rainforest, 600 m, Sieved Litter, QM Reg. No. T20046, EMEC1012182, ♀, QM. Bellenden Ker Range, 1 km S of Cable Tower, 6 Nov 3,1981, 500 m, EARTHWATCH/QLD MUSEUM, QM Berlesate 365, Rainforest, Sieved litter, QM Reg. T19997, EMEC1012204, ♀, QM.

Type locality. Queensland, Graham Range, 17° 17'S 145° 57'E.

Diagnosis. Nearly as small as *C. (F.) parva* but with shallowly crenulate elytral striae and the lateral bead of the pronotal not distinct in the basal third and entirely absent before reaching the basal seta (Fig. 39).

Description. *Size.* SBL 4.0–4.5 mm, greatest width over elytra 1.5–1.8 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes small, flattened. Ocular ratio 1.26–1.33. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 39): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly, shallowly emarginate, apical angles scarcely produced, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 13 or 14 setigerous punctures, two setigerous punctures

near apex of interval 7. Elytra: color rufopiceous, macrosculpture a few scattered small punctulae, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed shallowly, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1 with lateral sulcus, 1 medially and 2–5 without sulci or 1 with lateral and medial sulci, 2–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 64): orientation of median lobe of aedeagus in repose left side up. Female genitalia and reproductive tract (Fig. 78): apical margin of gonocoxite-1 with one seta, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 long, very slightly curved, narrowly rounded apex, bursa straight elongate, common oviduct inserted in apical cup, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) blatta sp. nov.
(Figs 14, 44, 81)

Etymology. The specific epithet *blatta* is based on the Latin for "a little insect", often referring to one that is cockroach-like in general form, which is appropriate for these beetles given their form and scuttling movement through the leaf litter. It is treated as a noun in the nominative singular standing in apposition.

Type material. HOLOTYPE, ♂. "Bellenden Ker Range, NQ Cable Tower, 1054 m Nov 1–7, 1981 EARTHWATCH"//"QLD MUSEUM. Pitfall trap in rainforest. QM Reg. No. T19998"//"EMEC1012202". Deposited QM. PARATYPES. Mount Bellenden Ker, eastern slope 1192 m. 8.xi.2009 K.Staunton [BK12K2A], EMEC1000448, ♀, QM. Same locality with 11.viii.2009 [BK12K2A], kww841, EMEC1000450, ♀, QM. Same locality with 1166 m. 15.ix.2009 [BK12K1B] kww838, EMEC1000449, ♀, QM. Bellenden Ker Range, Summit TV Stn 29 Apr - 2 May 1983 G.B.Monteith, D.K.Yeates QM Berlesate No. 571 17.16S 145.51E rainforest, 1560 m sieved litter QM Reg. T20021, EMEC1012201, ♀, QM. Bellenden Ker Range, Cable Tower 3, 1054 m Oct 17–24 1981 EARTHWATCH, QLD MUSEUM Pitfall trap in rainforest, QM Reg. T19995, EMEC1012203, ♀, QM. Mt. Bellenden Ker, R.S.Storey, Pitfall Nov 1977 to Jan 1978 5200', EMEC1000328, ♀, ANIC. Mt. Bellenden Ker R.S.Storey, Nov 1977–Jan 1978 5200', EMEC1012208, ♂, QDAF. Bellenden Ker, Cable tower No. 3 12 Apr 1979 G.B.Monteith, QM Berlesate 21, 17.16S, 145.52E Rainforest, 1000 m Sieved litter, QM Reg. T19985, EMEC1012205, ♂, QM. Bellenden Ker range, Cable tower No. 3, 1054 m Oct.25– 31,1981 EARTHWATCH, QLD MUSEUM QM Berlesate No. 326, 17.16S, 145.52E Rainforest, 1000 m, Sieved litter, QM Reg. T19996, EMEC1012206, ♂, QM.

Type locality. Queensland, Bellenden Ker Range. Estimated coordinates: 17° 16'S 145° 52'E.

Diagnosis. Fairly small sized beetles with a general form similar to the larger *C. (F.) iridescens* with a more extensive basolateral depressed region on the pronotum (Fig. 14).

Description. *Size.* SBL 4.7–5.8 mm, greatest width over elytra 1.9–2.2 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes small, flattened. Ocular ratio 1.20–1.34. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae,

apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 14): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent or present, short, shallow, broad, not well delimited, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle or to just apicad hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 9 with 14 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous or first interval slightly paler brunneous, especially near apex, margins slightly paler brunneous, otherwise deep brunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 44): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal with slight rotation to left, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view styliform throughout, apex of median lobe in lateral view erect dorsal hook, apex of median lobe in dorsal view narrowly rounded point. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with one seta or with two setae, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 moderately long, slightly curved, broadly rounded apex, bursa long, left directed curved form, common oviduct inserted near apex, right lateral portion of bursa with very large pouch, base broadly joined to bursa, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length very elongate, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) danbullaensis sp. nov.
(Figs 19, 47, 82)

Etymology. The specific epithet *danbullaensis* is based on the type locality near Mt. Haig in Danbulla National Forests and is treated as an adjective.

Type material. HOLOTYPE, ♂. "QLD, 1140 m nr. Mt Haig 30/vi/1971, Taylor Feehan"//"Berlesate ANIC. 349 rainforest 17.06x145.35"// "EMEC1000303", ANIC.

Type locality. Queensland, Mt Haig. Estimated coordinates: 17° 6'S 145° 35'E.

Diagnosis. Small size, notably elongate-oval shaped elytra, and flatly rounded anteroventral mesepisternum distinguish these beetles from other species. *Cerabilia Feronista haigensis* is sympatric with and very similar to, but notably larger than *C. danbullaensis*. While only subtly different in microsculpture (see key) the male genitalia (Figs 47, 54) are strikingly different between these species.

Description. *Size.* SBL 5.4 mm, greatest width over elytra 2.0 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.30. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, acutely pointed. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 19): microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle ended well apicad hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 9 with 14 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster moderately glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male straight. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire. *Male* genitalia (Fig. 47): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view broadly narrowed apex turned to left, apex of median lobe in lateral view broader at apex, reflexed ventrally, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract: female unknown.

Cerabilia (F.) gigas sp. nov.
(Figs 27, 52, 73, 74, 82)

Etymology. The specific epithet *gigas* is based on the Latin for a giant, one of the fabled offspring of Earth and Tartarus. It draws attention to the relatively large size of these beetles, and is treated as a noun in the nominative singular standing in apposition.

Type material. HOLOTYPE, ♂. "NE QLD, Upper Boulder Ck via Tully, 900 m 25–27 Oct 1983 Monteith, Yeates & Thompson, Dung trap in R[ain] F[orest]"//"QM Reg. No. T20024"//"EMEC1012222". Deposited QM. PARATYPES. Upper Boulder Ck., 1000 m, 11 km NNW of Tully, 16–19 Nov 1984. Cook, Monteith & Thompson, QM Reg. No. T20029, EMEC1012218, ♂, QM. Same with QM Reg. No. T20030, EMEC1012219 and QM Reg. No. T20031, EMEC1012220, 2♀♀, QM. Upper Boulder Ck via Tully, 27 Oct 1983, Monteith, Yeates & Thompson, QM Berlesate No. 618, Rainforest, 900 m, Sieved litter, QM Reg. No. T20026, EMEC1012221, ♀, QM.

Upper Boulder Ck via Tully, 900 m, 25–27 Oct 1983 Monteith, Yeates & Thompson, QM Reg. No. T20025, EMEC1012223, ♂, QM.

Type locality. Queensland, Upper Boulder Creek. Estimated coordinates: 17° 50'S 145° 54'E.

Diagnosis. Largest beetles in the genus. The narrow almost parallel-sided pronotum (Fig. 27) and dense micropunctulae across the elytral intervals distinguishes these beetles from other *Cerabilia* species.

Description. *Size.* SBL 9.1–11.5 mm, greatest width over elytra 3.1–4.0 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes small, flattened. Ocular ratio 1.31–1.52. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and few small scattered setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 27): microsculpture not or scarcely apparent at 50x magnification or sculpticells transversely elongate, longitudinally short relative to body axis, macrosculpture with very fine, scattered micropunctulae, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 9 with 16 or 17 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture distinct, dense irregularly punctulate, microsculpture not apparent at 50x magnification, luster dull. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture shallowly punctate or rugulose or lightly scabriculous. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 52): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view flattened with a clockwise twist, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view thick margin rounded not flexed, apex of median lobe in dorsal view blunt and slightly rounded. Female genitalia and reproductive tract (Figs 73–74): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 long, very slightly curved, narrowly rounded apex, bursa long, left directed curved form, common oviduct inserted near apex, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct

length very elongate, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa elongate, narrow diverticula with bulbous apex, ventral modification of bursa absent.

Cerabilia (F.) haigensis sp. nov.
(Figs 25, 54, 84)

Etymology. The specific epithet *haigensis* is based on the type locality Mt. Haig and is treated as an adjective.

Type material. HOLOTYPE, ♂. "Mt. Haig, QLD, 145.35S 17.06E, 30 June 1971, Taylor & Feehan"// "EMEC1000301". ANIC.

Type locality. Queensland, Mt. Haig, 17° 6'S 145° 35'E.

Diagnosis. Similar to *C. (F.) tipica* but smaller, with a narrower, more elongate form, and no basal impressions on the pronotum (Fig. 25). *Cerabilia Feronista danbullaensis* is sympatric with and very similar to *C. (F.) haigensis*. While subtly different in microsculpture (see key) the male genitalia are strikingly different (Figs 47, 54).

Description. *Size.* SBL 7.4 mm, greatest width over elytra 2.7 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.27. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, acutely pointed. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 25): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to just apicad hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals flat, widths all approximately equal, interval 9 with 16 or 17 setigerous punctures, two setigerous punctures three. Elytra: color rufopiceous, macrosculpture distinct, dense irregularly punctulate, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster moderately glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth or smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatibia of male straight. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half femur length, apically pointed, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire. *Male* genitalia (Fig. 54): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broadly narrowed apex turned to left, apex of median lobe in lateral view simple taper reflexed ventrally, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract: female unknown.

Cerabilia (F.) intermedia (Moore, 1965: 26)
(Figs 31, 58, 83)

Feronista intermedia Moore, 1965

Type material. Holotype, ♂. "N. QUEENSLAND: Mt. Bartle Frere, W. slope. 3-5000' [914–1524 m], Dec 57 (Darlingtons)". ANIC.

Specimens examined. Holotype and male paratype and three males and five females from the type locality examined (MCZ, ANIC, QM).

Diagnosis. Recognisable combination of medium to large size for genus with distinct spectral iridescence dorsally. Legs are pale except for the distinctly infuscated base of the femur.

Redescription. *Size.* SBL 7.0–8.8 mm, greatest width over elytra 3.1–3.3 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.29–1.31. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 31): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions present, short, shallow, broad, not well delimited, outer basal impressions present as a shallow, poorly defined, broad depression, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to beyond hind angle and onto base nearly to inner impression, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles nearly right angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth or smooth. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci, rarely 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 58): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 moderately long, slightly curved, broadly rounded apex, bursa straight, relatively stout, cup-shaped, right lateral portion of bursa elongate, ended in a spherical pouch, dorsal

development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) iridescens sp. nov.
(Figs 16, 45, 67, 81)

Etymology. The specific epithet *iridescens* is from Latin and refers to the iridescent dorsal surface of these beetles, and is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "NEQ: 16°55'Sx145°40'E Mt Williams, 900–1000 m 2–3 Dec 1993. Cook, Monteith & Janetzki"//"QM Reg. No. T20051"//"EMEC1012169", QM. PARATYPE. Same data as holotype and QM Reg. No. T20050, EMEC1012171, ♀, QM. AUS14 kww542.

Type locality. Queensland, east of Mt. Williams. 16° 55'S 145° 40'E.

Diagnosis. *Cerabilia Feronista iridescens* is distinguished from similar species above (*C. (F.) blatta, C. (F.) australiensis*) in that the male is more brilliantly iridescent than the female and the basolateral area of the pronotum (Fig. 16) has a smaller depressed region than these similar appearing species.

Description. *Size.* SBL 6.2–6.8 mm, greatest width over elytra 2.3–2.6 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, convex. Ocular ratio 1.30–1.39. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 16): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent or absent, but with broad, very shallow depressions, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. *Elytra*: color rufobrunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 45): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, blade of median lobe in ventral view broadly tapering, apex of median lobe in dorsal view blunt and slightly rounded. Female genitalia and reproductive tract (Fig.

67): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 long, very slightly curved, narrowly rounded apex, bursa straight, relatively stout, cup-shaped, right lateral portion of bursa relatively short and ended in a small rounded pouch, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate, rounded and slightly expanded apically, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) kalkajaka sp. nov.
(Figs 20, 48, 71, 82)

Etymology. The specific epithet *kalkajaka* is based on the name given by the eastern Kuku Yalanji Aboriginal people for the type locality (Black Mt., Qld.) and is treated as an adjective.

Type material. HOLOTYPE, ♂. "Black Mtn, 17 km ESE of Julatten, N.Qld 29 Apr. 1982 Monteith,Yeates & Cook"//"Q.M. BERLESATE No. 413, 16.39S 145.29E, Rainforest, 1000 m Sieved litter & moss"//"QM Reg. No. T20008"//"EMEC1012163". QM. PARATYPES. Same data as holotype, with 29–30 Apr. 1982, 800–1000 m Monteith, Yeates & Cook, QM Reg. No. T20009, EMEC1012164, ♂, QM, and QM Reg. No. T20010, EMEC1012165, ♀, QM.

Type locality. Queensland, Black Mtn. 16° 38'S 145° 29'E.

Diagnosis. Brilliantly iridescent, medium-sized beetles with rounded pronotum (Fig. 20) that lacks or has only a slight indication of a depressed basolateral region. These features and the prominently raised region of the anteroventral mesepisternum distinguishes these beetles from similar species.

Description. *Size.* SBL 6.7–7.3 mm, greatest width over elytra 2.4–2.6 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, convex. Ocular ratio 1.38–1.47. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 20): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly, shallowly emarginate, apical angles scarcely produced, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 14 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous or brunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed shallowly, where impressed, very small, shallowly punctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin obtusely angulate. Metatarsomeres 1 with lateral sulcus only, 2–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form longer than half femur length, acuminate to rounded point. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two

rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 48): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view styliform throughout, apex of median lobe in lateral view appressed dorsal hook, apex of median lobe in dorsal view blunt. Female genitalia and reproductive tract (Fig. 71): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa long, left directed curved form, common oviduct inserted near apex, right lateral portion of bursa elongate, ended in a spherical pouch, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length very elongate, gland duct diameter increasing apically, without notable expansion, gland form elongate, rounded and slightly expanded apically, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) lewisensis sp. nov.
(Figs 3, 35, 62, 79, 87)

Etymology. The specific epithet *lewisensis* is based on the type locality Mt. Lewis and is treated as an adjective.

Type material. HOLOTYPE, ♂. "QLD: 16.511°S x 145.296°E, Mt. Lewis Rd., hut, 12 km NW Julatten, 1187 m., 22 Nov 2009. Sieved Litter, Monteith & Turco. 18633"//"EMEC1000451". QM. PARATYPES. Same data as holotype with EMEC1000327 and EMEC1000300 , 2♀♀, QM. Same data as holotype with EMEC1000452 and EMEC1012207 AUS27 kww 843, 2♂♂, QM. Mt Lewis 29 km from Hwy, 29 Nov 1997 D.J. Cook, QM BERLESATE 964, Rainforest, 1210 m leaf litter, QM Reg. No. T66693, EMEC1012150, ♀, QM.

Type locality. Queensland, Mt. Lewis, 16° 30'S 145° 17'E .

Diagnosis. Distinct from all other species by the combination of the broad pale region laterally, apically, and along the length of interval 1 of the elytra (Fig. 3) and the well impressed, stretched microsculpture on the pronotum and elytra.

Description. *Size.* SBL 4.7 mm, greatest width over elytra 1.7 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes small, flattened. Ocular ratio 1.26. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 35): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 16 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color first interval distinctly paler brunneous, broadly pale along apex, margins slightly paler, otherwise castaneous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster moderately glossy.

Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1 with lateral sulcus only, 2–3 with lateral and medial sulci, 4–5 without sulci. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 62): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and narrowly pointed, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view small ventral tooth, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract (Fig. 79): apical margin of gonocoxite-1 with one seta, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 moderately long, slightly curved, broadly rounded apex, bursa long, right directed curved form, common oviduct inserted near apex, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length short, gland duct with notable expanded region near base of gland, gland form elongate, rounded and slightly expanded apically, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) loxandroides sp. nov.
(Figs 23, 72, 85)

Etymology. The specific epithet *loxandroides* draws attention to the similar form of these beetles to some species of *Loxandrus*. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♀. "NE. Q: 16°22'S x 145°13'E, 7 km N. Mt Spurgeon (Camp 2), 17–19 Oct 1991, 1200–1250 m, Monteith, Janetzki, Cook & Roberts"//"QM Reg. No. T20049"//"EMEC1012135". QM.

Type locality. Queensland, Mt. Spurgeon, 16° 22' E 145° 13'S.

Diagnosis. Large, dull beetles. Larger and with a more quadrate pronotum (Fig. 23) than *C. (F.) moorei*. The distinct, dull, isodiametric elytral microsculpture separate this species from others that are of similar size or larger, e.g. *C. (F.) gigas* and *C. (F.) intermedia*.

Description. *Size.* SBL 9.0 mm, greatest width over elytra 3.2 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes small, slightly convex. Ocular ratio 1.26. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 23): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly, shallowly emarginate, apical angles scarcely

produced, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals flat, widths all approximately equal, interval 9 with 18 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture smooth, microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, luster dull. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture smooth, rarely very lightly scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire. Male genitalia: male unknown. Female genitalia and reproductive tract (Fig. 72): apical margin of gonocoxite-1 with one seta, lateral edge of gonocoxite-2 with two ensiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa left to right recurved, oviduct inserted near apex in posterior facing groove, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) minor (Moore, 1965: 26)

(Figs 12, 42, 81)

Feronista minor Moore, 1965

Type material. HOLOTYPE, ♂. "N. QUEENSLAND: Mt. Spec Plateau, 2–3000 feet, xi.57 (Darlingtons)". ANIC.

Diagnosis. Small beetles with a form and size similar to *C. (F.) blatta*. Recognisable from that species and other small *Cerabilia* by the much more narrowly angled (though still obtusely so) hind angles of the pronotum (Fig. 12).

Redescription. *Size.* SBL 5.5–5.8 mm, greatest width over elytra 2.1 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes small, flattened. Ocular ratio 1.26. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 12): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 9 with 14 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly

angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally glabrous. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire. *Male* genitalia (Fig. 42): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal or dorsal with slight rotation to left, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view narrowly rounded point. Female genitalia and reproductive tract: female unknown.

Cerabilia (F.) monteithi (Baehr, 2007: 6)

(Figs 38, 63, 89)

Australomasoreus monteithi Baehr, 2007

Type material. HOLOTYPE, ♂. " Forest Station, 2000 feet, Bulburin State Forest via Many Peaks, Qld. 12–15.iv.1974 G.B.Monteith"//"UQIC Reg. #90482 (QM T123808)" QM.

Specimens examined. A total of 11 specimens from the type locality examined, seven males and four females, EMEC.

Diagnosis. This species is similar to, but much smaller than the sympatric *C. (F.) amaroides* and it lacks the elytral humeral tooth found in *C. (F.) amaroides*. It is notably less oval than the similar looking *C. (F.) oodiformis*. The elytral striae are very shallowly impressed and usually only represented by punctures for most of their length.

Redescription. *Size.* SBL 5.2–5.6 mm, greatest width over elytra 2.2–2.3 mm. *Head.* Dorsal microsculpture not apparent at 50x magnification. Eyes average size, somewhat flattened. Ocular ratio 1.22–1.32. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 pubescent in apical 1/3–1/2. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 38): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to beyond hind angle, onto base to near midline, basal margin very shallowly emarginate in middle, anterior margin medially deeply, broadly emarginate, apical angles large, prominent, hind angles completely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 16 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster moderately glossy or glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed very shallow or not impressed, except near apex and apical third of 5–8, where impressed, shallow, elongate punctulae. Metepisternum macrosculpture rugulose or lightly scabriculous. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1 with lateral sulcus, 1 medially and 2–5 without sulci or 1 with lateral and medial sulci, 2–5

without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1 with lateral sulcus only, 2–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. Defensive gland chemical compounds from defensive glands formic acid, decane, undecane or 2-pentadecanone. *Male* genitalia (Fig. 63): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view arcuate and curved ventrally, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view blunt. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with three setae, lateral edge of gonocoxite-2 with two ensiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa very short, right lateral portion of bursa with very large pouch, base broadly joined to bursa, dorsal development of bursa lacking, spermatheca very short sessile, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate, rounded and slightly expanded apically, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) montivaga sp. nov.
(Figs 13, 43, 66, 81)

Etymology. The specific epithet *montivaga* is based on the Latin for "mountain-roaming" and indicates the habitat where this species is found. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "Mt. Father Clancy, 9 km S. Milla[a] Milla[a], N.Qld. 6–14 Dec 1988, 800 m Monteith & Thompson, Pitfall Traps"//"QM Reg. No. T20038"//"EMEC1012232". QM. PARATYPES. Vine Creek, Majors Mt. 4–6 Feb 1999. 1060 m G.Monteith & D.Cook, fish pitfall, rainforest, QM Reg. No. T78990, EMEC1012216 AUS11 kww539, ♂, QM. Mt Kooroomooi, summit 7 kms. 3–4 Dec 1998 Monteith, Cook & Bouchard, 1050 m, Rainforest, QM Reg. No. T69248, EMEC1012217, ♀ QM.

Type locality. Queensland, Mt. Father Clancy. Estimated coordinates 17° 35'S 145° 38'E.

Diagnosis. Beetles of this species are fairly small, similar in size and body form to *C. (F.) minor* and *C. (F.) blatta*. *Cerabilia Feronista montivaga* has a more broadly rounded pronotum (Fig. 13) than these species and rounded hind angles, distinct from the obtusely angled hind angles in *C. (F.) minor* (Fig. 12).

Description. *Size.* SBL 4.5–5.2 mm, greatest width over elytra 2.1–2.2 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, convex. Ocular ratio 1.25–1.27. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 13): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle,

anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 13 or 14 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous or brunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture rugulose or lightly scabriculous. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 43): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view short and broad, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract (Fig. 66): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa straight, relatively stout, cup-shaped, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa large, somewhat sclerotized pouch set in a depression.

Cerabilia (F.) moorei sp. nov.

(Figs 24, 51, 86)

Etymology. The specific epithet *moorei* is treated as a noun in the genitive case and is in honor of Dr. B.P. Moore, biochemist and carabidologist who described the genus *Feronista* and took me on my first trip up Mt. Lewis Road in 2004, where I collected my first specimen of *Cerabilia*, which is part of the type series

Type material. HOLOTYPE, ♂. "29 km up Mt Lewis Rd. via Julatten, N. Qld., 9–23.xi.1982, Morgan, Brown, Storey. MDPI Intercept Trap, Site No. 4"//"QM Reg. No. T20012" //"EMEC1012142". QM. PARATYPES. Mount Lewis Road, pitfall 940 m., 23.vi-30.vii.2008 K.Staunton, CU10A6, 346181, EMEC1000469; same data with CU10A6, C 3455B1, EMEC1000470, 2♀♀, QM. Mount Lewis Road, 1160 m. 3.i.2009 K.Staunton, [CU12A6C], EMEC1000479, ♂, QM. Mount Lewis Road, pitfall 23.vi-30.vii.2008, K.Staunton, CU10A6C, EMEC1000474, ♂, QM. Mount Lewis, Road, baited pitfall, 4.viii-31.viii.2007, K.Staunton, CH12A2, EMEC1000475, ♂, QM. Mount Lewis Road, baited pitfall 4.viii-31.viii.2007, K.Staunton, CH12A2, EMEC1000476, ♂, QM. Mount Lewis Road, pitfall 1016 m. 23.vi-30.vii.2008, K.Staunton, CU10A2 C 3437B2, EMEC1000497, ♂, QM. 7.5 km N Mt Lewis, via Julatten, 8 Sept 1981, G.Monteith & D.Cook, Q.M. BERLESATE No. 279, Rainforest, 1200 m, Sieved Litter, QM Reg. No.T19988, EMEC1012143, ♂, QM. Mt Lewis 1000 m, 15.iv.90, B.P. Moore, EMEC1000478 and EMEC1000495, 2♂♂, ANIC. Mt. Lewis via Julatten, 8 Mar. 1985, A.Walford-Huggins, mine site, ex leaf litter, EMEC1000477, ♀, ANIC. 29 km up Mt Lewis Rd. via Julatten, 9–23.xi.1982, Morgan, Brown, Storey, MDPI Intercept Trap, Site no. 4, EMEC1012139, ♂, QPID. Same locality with EMEC1012138; EMEC1012140 and EMEC1012141,

3♀♀, QPID. Mt. Lewis, 29.x.1980, R.Storey, G. Strickland, Berleseate, EMEC1012144, ♀, QPID. Mt. Lewis Rd., hut, 12 km NW Julatten, 1187 m., 22 Nov 2009, Sieved Litter, Monteith & Turco, 18633, in EtOH, EMEC1000499, ♀, EMEC. Mount Lewis Road, hut, 12 km northwest of Julatten, 1187 m. 8.viii.2004, K.Will & B.P.Moore, in EtOH, EMEC1000498 AUS2 kww250, ♂, EMEC. Same locality with, 1200 m, leaf litter, EMEC1012146 and EMEC1012147, 2♀♀, EMEC.

Type locality. Queensland, Mt. Lewis. Estimated coordinates 16° 30'S 145° 16'E.

Diagnosis. Large sized beetles with distinct dorsal microsculpture (shallower in males) and in most specimens the first elytral interval, and narrowly along the lateral margins, paler. Similar in form, but smaller than *C. (F.) loxandroides* and with a notably narrower pronotum (Fig. 24).

Description. *Size.* SBL 6.1–7.4 mm, greatest width over elytra 2.2–2.6 mm. *Head.* Dorsal microsculpture not apparent at 50x magnification. Eyes average size, convex. Ocular ratio 1.24–1.32. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 24): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals flat, slightly more convex near apex, 7 and 8 distinctly convex, subcarinate in apical third, widths all approximately equal, interval 9 with 16 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color first interval distinctly paler brunneous, margins slightly paler brunneous, otherwise infuscated black or deep brunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, luster dull. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin obtusely angulate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 51): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view arcuate, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view erect dorsal hook, apex of median lobe in dorsal view narrowly rounded point. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa left to right recurved, oviduct inserted near apex in posterior facing groove, right lateral portion

of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) mudda sp. nov.
(Figs 30, 57, 82)

Etymology. The specific epithet *mudda* is based on an abbreviated form of Muddamuddanaymy the Bandjin Aboriginal word for the type locality (Hinchinbrook Island) and is treated as a noun in apposition.

Type material. HOLOTYPE, ♂. "Hinchinbrook Is. NE Qld. Upper Gayundah Ck. 850 m 9–11 Nov 1984. R.F. G.Monteith & D.Cook"//"QM Reg. No. T20028"//"EMEC1012231". QM.

Type locality. Queensland, Hinchinbrook Island, Upper Gayundah Creek. Estimated coordinates 18° 21'S 146° 14'E.

Diagnosis. Piceous to black, smooth, iridescent with piceous legs and antennae. Similar in luster and color to *C. (F.) amaroides*, but smaller, much narrower, and more convex form.

Description. *Size.* SBL 8.2 mm, greatest width over elytra 3.2 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes small, flattened. Ocular ratio 1.25. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 30): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle ended well apicad hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals flat, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin obtusely angulate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire. *Male* genitalia (Fig. 57): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal or dorsal with slight rotation to left, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view styliform at tip, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded.

Female genitalia and reproductive tract: female unknown.

Cerabilia (F.) oodiformis sp. nov.
(Figs 5, 34, 61, 80, 90)

Etymology. The specific epithet *oodiformis* is a Latin compound word drawing attention to the egg-shaped form of these beetles and that they are similar to beetles in the genus *Oodes* Bonelli. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "MEQ: 21°36'S ×148°58'E, Blue Mt., 0.6 km SE, 3–4 Oct 1999, 800–1058 m, Monteith, Cook, Burwell, Evans. Rain forest, 7801"//"EMEC1012245". QM. PARATYPES. Blue Mt. summit, 1058 m, 30 May 2000. Burwell, Cook & Monteith, rainforest, 9275, EMEC207006, ♀, QM. Blue Mt. 0.6 km SE 3– 4 Oct 1999, 800–1058 m, Monteith, Cook, Burwell & Evans. rainforest, 7801, EMEC1012243, ♂, QM. Blue Mt. 0.6 km SE, 930 m 23 Mar–30 May 2000 Monteith & Cook, rainforest, pitfall 9422, EMEC1012244, ♀, QM. Blue Mt. 0.6 km SE 3– 4 Oct 1999. 800–1058 m Monteith, Cook, Burwell & Evans. Rainforest 7801 QM Reg. No. 94946, EMEC214586, ♀, QM. Same data with QM Reg. No. 94947, EMEC214588; QM Reg. No. 94948, EMEC214587 and QM Reg. No. 94945, EMEC214589, 3♂♂, QM. Eungella, about 3 km S., about c.780 m, 26.iii.1975, R.W.Taylor, EMEC1000472, ♂, ANIC. Eungella National Park, Peases Lookout rainforest, 820 m, 13.i.2008, K.Will [AUS2008.i.13.2] in EtOH, AUS5 EMEC207007 kww494, ♂, EMEC. Eungella NP rainforest 1020 m. 13.i.2008 K.Will [AUS2008.i.13.3], EMEC1000494, ♀, EMEC.

Type locality. Queensland, Blue Mt., 21° 36'S 148° 58'E.

Diagnosis. The distinctly oodine-like body form (Fig. 5) and very prominent elytral humeral tooth distinguishes this species from all others in the genus.

Description. *Size.* SBL 5.9–7.5 mm, greatest width over elytra 2.6–3.0 mm. *Head.* Dorsal microsculpture not apparent at 50x magnification. Eyes small, flattened. Ocular ratio 1.22–1.29. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 34): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, broader across base than apex, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 16 setigerous punctures, two setigerous punctures near apex of interval 7 or three. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Humeri distinct denticle. Elytral striae impressed shallowly apically and not impressed in basal 5th, 5–7 very shallow on disc, where impressed, very small, shallowly punctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male slightly arcuate. Metatarsomeres 1 with lateral sulcus only, 2–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 61): orientation of median lobe of

aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view arcuate, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract (Fig. 80): apical margin of gonocoxite-1 with one seta or with two setae, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa short, left directed, common oviduct inserted near apex, right lateral portion of bursa with very large pouch, base broadly joined to bursa, dorsal development of bursa lacking, spermatheca not evident, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected to common oviduct, gland duct with notable expanded region near base of gland, gland form elongate, rounded and slightly expanded apically, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) parva sp. nov.
(Figs 18, 69, 81)

Etymology. The specific epithet *parva* is Latin for small and this refers to the very small size of these beetles. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♀. "QLD. 730 m Mt Tiptree 29/vi/1971 Taylor Feehan"//"EMEC1000471". ANIC.

Type locality. Queensland, Mt. Tiptree. Estimated coordinates 17° 5' S 145° 37'E.

Diagnosis. Recognisable by the minute size. These are the smallest beetles in *Feronista* and as small as any species in the genus. The elytra are rather convex and relatively short.

Description. *Size.* SBL 3.9 mm, greatest width over elytra 1.7 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.25. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 18): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin straight, anterior margin medially broadly, shallowly emarginate, apical angles scarcely produced, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 14 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture smooth, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 18): male unknown. Female genitalia and reproductive tract (Fig. 69): apical margin of gonocoxite-1 with one seta, lateral edge of gonocoxite-2 glabrous, apical furrow of

gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa short, left directed, common oviduct inserted near apex, right lateral portion of bursa with relatively short pouch, dorsal development of bursa lacking, spermatheca short, width at middle 2/3 total length, spermatheca duct as wide as reservoir and twice reservoir length, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) prolixa sp. nov.
(Figs 33, 60, 88)

Etymology. The specific epithet *prolixa* is from the Latin for "wide" and refers to broad form of the body in these beetles, and is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "Devil's Thumb - Paul Luck, 12 km WNW Mossman, NQ, 27 Dec 1989 - 15 Jan 1990, ANZSES Expedition, Site 11, 1240 m, pitfall"//"QM Reg. No. T20044"//"EMEC1012151". QM.

Type locality. Queensland, 12 km west-northwest of Mossman. Estimated coordinates: 16° 24'S 145° 17'E.

Diagnosis. These distinctive beetles are similar to *C. (F.) prosopogmoides*. See the diagnosis under that species.

Description. *Size.* SBL 6.0 mm, greatest width over elytra 2.3 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, convex. Ocular ratio 1.32. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 33): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, but with broad, very shallow depressions, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, broader across base than apex, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles nearly right angled, rounded not sharp, anteriolateral setae distant from lateral margin, about 2x width of setal pore from lateral margin. Elytron with ten intervals, form of intervals flat, slightly more convex near apex, widths widest point of 3rd notably wider than 2nd, approximately 1.6x width of 2nd, 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture shallowly punctate. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male straight. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form obtusely truncate with rounded point. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire. *Male* genitalia (Fig. 60): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in

dorsal view broadly rounded. Female genitalia and reproductive tract: female unknown.

Cerabilia (F.) prosopogmoides sp. nov.
(Figs 32, 59, 88, 147)

Etymology. The specific epithet *prosopogmoides* draws attention to the similar form of these beetles to some species of *Prosopogmus* Chaudoir. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "16°32′32.3″S /145°17′03.7″E, AUSTRALIA: Queensland, Mt. Lewis, headlamp search, 974 m., 19.xii.2010, K.Will [AUS2010.xii.19.2]" //"EMEC207000". QM. PARATYPES. Same data as holotype with EMEC1000466 and EMEC207001, 2♂♂, EMEC; EMEC207003, ♂, ANIC; EMEC207004, ♂, QM. Same data as holotype with EMEC1000467, EMEC1000468, EMEC215152 AUS16 kww842, 3♀♀, EMEC; EMEC1005896, ♀, ANIC; EMEC207002 and EMEC207005, 2♀♀, QM. Mount Lewis Road, pitfall 1181 m., 23.vi-30.vii.2008, K.Staunton CU12A4 B 3424B2, EMEC1000496, ♀, QM.

Type locality. Queensland, Mount Lewis, 16° 32'S 145° 17'E.

Diagnosis. This species and *C. (F.) prolixa* share a body form distinct in the genus. Both are broad across the elytral humeri and pronotal base. The pronotum (Fig. 32) is widely depressed from the base, narrowing to the midpoint of the pronotal length. The anterior lateral punctures are set far from the margin. *Cerabilia Feronista prosopogmoides* males are recognisable by the deep, dorsal concavity of the meta femur (Fig. 147) lacking in *C. (F.) prolixa* males.

Description. *Size.* SBL 6.6–7.1 mm, greatest width over elytra 2.5–2.9 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.30–1.43. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 32): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions present, short, shallow, broad, not well delimited or present, short, shallow, clearly marked, outer basal impressions present as a shallow, poorly defined, broad depression, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle ended well apicad hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially deeply, broadly emarginate, apical angles large, prominent, hind angles nearly right angled, rounded not sharp, anteriolateral setae distant from lateral margin, about 2x width of setal pore from lateral margin. Elytron with ten intervals, form of intervals flat, slightly more convex near apex, widths widest point of 3rd notably wider than 2nd, approximately 1.6x width of 2nd, 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture shallowly punctate. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male straight. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to greater than half femur length, apically pointed, dorsally deeply concave in male (Fig. 147), convex in female. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with

two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 59): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with one seta, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, bluntly rounded apex, bursa short, straight, common oviduct entering on left lateral side, right lateral portion of bursa elongate, ended in a spherical pouch, dorsal development of bursa lacking, spermatheca very short sessile, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at posterior oriented apex, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) reflexa sp. nov.
(Figs 22, 50, 85)

Etymology. The specific epithet *reflexa* is from the Latin for "recurved" and refers to the form of aedeagus tip. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "NE QLD, The Bluff, 11 km W of Mossman, 27 April 1983, G.B.Monteith, D.K.Yeates, QM BERLESATE No. 552, 16.27S 145.16E, rainforest, 1050 m, moss"//"QM Reg. No. T20013"//"EMEC1012162". Deposited QM. PARATYPES. Mossman Bluff Track, 5–10 km W Mossman, 17–31 Dec 1988, Monteith, Thompson & ANZSES Site 10, 1300 m, flight intercept, QM Reg. No. T20040, EMEC1012156, ♀. QM. Mossman Bluff, summit 10 km W Mossman, 18 Dec 1988, 1300 m, G.Monteith & G.Thompson, pyrethrum/trees & rocks, QM Reg. No. T20041, EMEC1012159, ♀, QM. 7.5 km N Mt Lewis, via Julatten, 8 Sept 1981 G.Monteith & D.Cook, Q.M. BERLESATE No. 279 Rainforest, 1200 m Sieved litter, QM Reg. No. T19986, EMEC1012148, ♂. QM. Same locality with QM Reg. No. T19987, EMEC1012149, ♀, QM.

Type locality. Queensland, The Bluff, 11 km west of Mossman, 16° 27'S 145° 16'E.

Diagnosis. Small parallel-sided beetles with distinctly dull elytral microsculpture and contrastingly pale legs that usually have the tibiae infuscated. In form and size similar to *C. (F.) lewisensis,* though the color and microsculpture are distinctively different.

Description. *Size.* SBL 4.2–5.4 mm, greatest width over elytra 1.6–1.8 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.20. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 22): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals flat, slightly more convex near apex, 7 and 8 distinctly convex, subcarinate in apical third, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color first interval

distinctly paler brunneous, margins slightly paler brunneous, otherwise infuscated black or deep brunneous, macrosculpture smooth, microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, luster dull or moderately glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth or smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. Male genitalia: orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view arcuate, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view erect dorsal hook, apex of median lobe in dorsal view narrowly rounded point. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with one seta or with two setae, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, bluntly rounded apex, bursa long, right directed curved form, common oviduct inserted near apex, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length very elongate, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) securilata sp. nov.
(Figs 10, 40, 65, 81)

Etymology. The specific epithet *securilata* is based on the Latin for "in form of a hatchet", from Plinius' Natural History, and refers to the hatchet-shaped sclerite on spermatheca, and is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "Upper Boulder Ck., 11 km NNW of Tully, N. Qld. 17–18 Nov 1984, Davies, Monteith, Gallon, Cook & Thompson. Pitfalls 850–1000 m"//"QM Reg. No. T20033"//"EMEC1012224". Deposited QM. PARATYPES. Same data as holotype with EMEC1012225, QM Reg. No. T20034, ♀, QM. EMEC1012226, QM Reg. No. T20034, ♀, QM, EMEC1012227, 10 km N of Tully, 4–5 Dec 1989, 800 m Monteith,Thompson & Janetzki, QM Reg. No. T20042, EMEC1012228, ♀, QM; 1000 m, 16–19 Nov 1984. Cook, Monteith & Thompson, QM Reg. No. T20032, ♂, QM.

Type locality. Queensland, Upper Boulder Creek. Estimated coordinates 17° 49'S 145° 54'E.

Diagnosis. Beetles of this species are of similar, elongate form as found in *C. (F.) spuh*, *C. (F.) blatta*, and *C. (F.) iridescens*. They are much larger than *C. (F.) blatta* and *C. (F.) iridescens* and also not as brilliantly iridescent as the latter. The relatively narrower pronotum (Fig. 10), with distinct basal impressions, separates this species from the similarly sized *C. (F.) spuh* (Fig. 11).

Description. *Size.* SBL 7.2–7.8 mm, greatest width over elytra 2.6–2.8 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, convex. Ocular ratio 1.30–1.44. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 pubescent in apical 1/3–1/2. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose,

with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 10): microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, macrosculpture smooth, rarely with very fine, scattered micropunctulae, inner basal impressions absent, present, shallow, but defined medially, not delimited laterally, blending into broad depression or present, short, shallow, clearly marked, outer basal impressions absent or present as a shallow, poorly defined, broad depression, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles completely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color first interval slightly paler brunneous, especially near apex, margins slightly paler brunneous, otherwise deep brunneous, macrosculpture distinct, dense irregularly punctulate or irregular mix of slightly larger and many smaller punctulae, microsculpture not apparent at 50x magnification, lustre moderately glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally with fine, short, scattered setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 40): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper reflexed ventrally, apex of median lobe in dorsal view blunt.

Female genitalia and reproductive tract (Fig. 65): apical margin of gonocoxite-1 with one seta or with two setae, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 moderately long, slightly curved, broadly rounded apex, bursa straight elongate, common oviduct inserted in apical cup, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile sclerotized, crest-shaped, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) spinifer sp. nov.
(Figs 37, 86)

Etymology. The specific epithet *spinifer* is from the Latin "to bear thorns" and alludes to the spiny meso- and metatibiae in this and other *Cerabilia* species. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♀. "NEQ: 16°27′S ×145°11′E, Mt Spurgeon, 3 km S 19–23 Nov 1997, 1632

Monteith, Cook & Burwell, Sclerophyll Forest"//"QM Reg. No. T66694"//"EMEC1012137", QM.

Type locality. Queensland, Mt. Spurgeon, 16° 27'S 145° 11'E.

Diagnosis. Somewhat dull reflectance due to prominent microsculpture on the upper surface. Compact ovoid form like *C. (F.) wunduensis*, but with distinctly, though only slightly, narrowed pronotal width in the basal third (Fig. 37).

Description. *Size.* SBL 5.0 mm, greatest width over elytra 2.0 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, convex. Ocular ratio 1.35. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 37): microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins convergent in basal half, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles nearly right angled, rounded not sharp, anteriolateral setae distant from lateral margin, about 2x width of setal pore from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster moderately glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture rugulose or lightly scabriculous. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1 with lateral sulcus only, 2–3 with lateral and medial sulci, 4–5 without sulci. Metatarsomeres 1 with lateral sulcus only, 2–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Female protarsomeres 1–4 dorsally glabrous form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire. Male genitalia: male unknown. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with one seta, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, falcate, narrowly rounded apex, bursa straight elongate, common oviduct inserted in apical cup, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) spuh sp. nov.
(Figs 11, 41, 81)

Etymology. The specific epithet "spuh" is an arbitrary combination of letters treated as a noun in apposition.

Type material. HOLOTYPE, ♂. "NEQ 17°23'S ×145°46'E Bartle Frere. W Base 25 Nov 1994–10 Jan 1995 Monteith & Hasenpusch, Pitfall traps, 700 m"//"QM Reg. No. T22454"// "EMEC1012209". QM. PARATYPES. Mt Bartle Frere. West Slopes, 800–1000 m, 30 Dec 1989, G.B.Monteith, QM Reg. No. T20045, EMEC1012210, ♂, QM. NE Mt Bartle Frere, upper boulder caves, 25 Nov 1994. G.Monteith, QM BERLESATE No. 880, Rainforest, 1000 m, Sieved litter QM Reg. No. T22455, EMEC1012211, ♀, QM.

Type locality. Queensland, west base of Mt. Bartle Frere, 17° 23'S 145° 46'E.

Diagnosis. Similar to *C. (F.) securilata* (see diagnosis under that species). The broadly rounded lateral margins of the pronotum with reflexed basolateral area and lack of impressions is distinctive (Fig. 11).

Description. *Size.* SBL 7.6–8.9 mm, mm, greatest width over elytra 2.6–2.9 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.13–1.37. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 pubescent in apical 1/3–1/2. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form truncate at apex, edge shelf-like, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 11): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles completely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture irregular mix of slightly larger and many smaller punctulae, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 41): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view arcuate, blade of median lobe in ventral view styliform throughout, apex of median lobe in lateral view erect dorsal hook, apex of median lobe in dorsal view blunt. Female genitalia and reproductive tract: apical margin of gonocoxite-1 glabrous, lateral edge of gonocoxite-2 glabrous, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, bluntly rounded apex, bursa straight elongate, common oviduct inserted in apical cup, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile sclerotized, crest-shaped, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) storeyi sp. nov.
(Figs 4, 17, 46, 68, 82)

Etymology. The specific epithet *storeyi* is treated as a noun in the genitive case and is in honor of the

late Dr. Ross I. Storey, of Queensland, Australia for his contributions to entomology and as a collector of specimens in the type series.

Type material. HOLOTYPE, ♂. "Bellenden Ker Range, NQ. Summit TV station 29 Apr–2 May 1983, G.B. Monteith & D.K.Yeates"//"QM Berlesate No. 565, 17.16S 145.51E, 1560 m litter"//"QM Reg. T20017"//"EMEC1012187". QM. PARATYPES. Same data as holotype with QM Reg. No. T20018, EMEC1012190, ♂, QM. QM Berlesate No. 565, EMEC1012186, ♂, QM. QM Berlesate No. 565 QM Reg. T20016, EMEC1012185, ♂, QM. QM Berlesate No. 566, sieved litter, QM Reg. No. T20019, EMEC1012189, ♂, QM. QM Berlesate No. 572, sieved litter, QM Reg. No. T20020, EMEC1012188, ♀, QM. QM Reg. No. T20014, EMEC1012192, ♀, QM. QM Reg. No. T20015, EMEC1012191, ♀, QM. Bellenden Ker, eastern slope 1192 m. 16.xii.2009 K.Staunton [BK12K2B], EMEC1000465, ♀, QM. Eastern slope 1479 m. 14.ix.2009 K.Staunton [BK14K2B], EMEC1000462, ♀, QM. Eastern slope 1509 m. 6.x.2009 K.Staunton [BK14K3B], kww839, EMEC1000463, ♀, QM. Eastern slope baited pitfall, 1479 m. 2.i.2007–8. ii.2007 K.Staunton [BK14K2], EMEC1000454, same EMEC1000455, 2♂♂, QM. Eastern slope baited pitfall 1479 m. 2.viii.2007–30.viii.2007 K.Staunton [BK14K2], EMEC1000453, same EMEC1000458, 2♀♀, QM. Eastern slope baited pitfall 1479 m. 6.i.2007–8. ii.2007 K.Staunton [BK14K2], EMEC1000456, same EMEC1000457 and EMEC1000459, 2♀♀, 1♂, QM. Massey Range, 12 km S of Gordonvale, 2 May 1983, G.B.Monteith & D.Cook, QM Berlesate No. 573, rainforest, 1300 m sieved litter QM Reg. No. T20022, EMEC1012199 and same with QM Reg. No. T20023, EMEC1012200, 2♂♂, QM. Bellenden Ker Range, Summit TV Stn Apr-2 Oct 1982, 1560 m, S.Montague, Rainforest Pitfall trap, QM Reg. T20004, EMEC1012196 and same with QM Reg. No. T20005, EMEC1012195, QM Reg. No. T20006, EMEC1012194, QM Reg. T20007, EMEC1012193, 4♂♂, QM. Mount Bellenden Ker Ridge 1535 m. 6.x.2009 K.Staunton [BK16K1A], kww837, EMEC1000461, ♀, QM. Mt. Bellenden Ker Centre Peak summit, 10–12 Apr 1979 1500 m, G.B.Monteith, QM Reg. No. T19984, EMEC1012197, ♂, QM. Mt. Bellenden Ker Range, summit 1560 m, 1–30 Apr 1982, S. Montague, pitfall trap, QM Reg. No. T20003, EMEC1012198, ♀, QM. East of Massey Range, 4 km W of Centre Bellenden Ker, 9–11 Oct 1991. 1250 m, Monteith, Janetzki & Cook, QM Reg. No. T20047, EMEC1012183, ♂, QM. Same with QM Reg. No. T20048, EMEC1012184, ♀, QM. Mt. Bellenden Ker R.S.Storey, Pitfall Nov 1977 to Jan 1978, 1584 m, EMEC214451, ♀, QDAF. Bellenden Ker Range, Summit TV station 29 Apr–2 May 1983, G.B. Monteith & D.K. Yeates, QM Berlesate No., 1560 m litter, EMEC1000460, ♂, ANIC. Mt. Bellenden Ker E. side, 1371 m, Jan 58, P.J. Darlington, EMEC1000464, ♀, ANIC.

Type locality. Queensland, Bellenden Ker Range, 17° 16'S 145° 51'E.

Diagnosis. Beetles of this species are distinguished by the relatively large, distinctive, slightly transverse pronotum with narrowly rounded, but obtuse, hind angles, and well-impressed, linear basal pronotal impressions (Fig. 17).

Description. *Size.* SBL 7.0–8.0 mm, greatest width over elytra 2.5–3.1 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.23–1.28. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and few small scattered setae, apical palpomeres glabrous. Glossal sclerite form truncate at apex, edge shelf-like, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 17): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions present, linear, sharp, straight, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color brunneous, macrosculpture distinct, dense irregularly punctulate or many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster moderately glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately,

where impressed, impunctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 46): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view arcuate, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract (Fig. 68): apical margin of gonocoxite-1 with one seta, lateral edge of gonocoxite-2 with one ensiform seta, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa long, left directed curved form, common oviduct inserted near apex, right lateral portion of bursa elongate, horn-shaped, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (F.) stylata sp. nov.
(Figs 26, 56, 82)

Etymology. The specific epithet *stylata* is from the Greek *styl-*, "in the form of a pillar" and *-ata*, "to have" and this refers to the form of the males' aedeagus. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "Kirrama Rge. v[ia]Cardwell, NQ 2-3000′ Dec57 Darlingtons" //"EMEC1000302. ANIC.

Type locality. Queensland, Kirrama Range, near Cardwell. Estimated coordinates: 18° 6'S 145° 42'E.

Diagnosis. Small, convex beetles similar to *C. (F.) wunduensis* and *C. (F.) danbullaensis* but with distinct, though stretched and iridescently reflective, microsculpture.

Description. *Size.* SBL 5.6 mm, greatest width over elytra 2.2 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.33. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres plurisetose, with scattered short setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, acutely pointed. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 26): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with

ten intervals, form of intervals flat, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color brunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen*. Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire. *Male* genitalia (Fig. 56): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal with slight rotation to left, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view styliform throughout, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view narrowly rounded point. Female genitalia and reproductive tract: female unknown.

Cerabilia (F.) tipica sp. nov.
(Figs 28, 53, 75, 76, 83)

Etymology. The specific epithet *tipica* is from Latin alluding to this being a very typical looking species in the genus. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE. ♂. "Lambs Head, 10 km W Edmonton, N. Qld. 10–12 Dec 1989, 1200 m Monteith, Thompson, Janetzki"//"QM Reg. No. T20043"//"EMEC1012174". QM. PARATYPES. Emerald Creek, Lamb range, 11 Oct 1982, 950 m, Monteith, Yeates & Thompson, QM Reg. No. T20011, EMEC1012175, ♂, QM. Kauri Ck, Lamb range, 22 Apr 1997, 1000 m, G.B.Monteith, QM Reg. No. T69247, EMEC1012177, ♀, QM. Lamb Range, 19 km SE Mareeba, 11 Dec 1988, 1200 m, Monteith, Yeates & Thompson, QM Reg. No. T20039, EMEC1012176, ♀, QM.

Type locality. Queensland, Lambs Head, Estimated coordinates 17° 1'S 145° 38'E.

Diagnosis. Distinctive beetles that are large size, robustly built, with broadly rounded pronotal margins (Fig. 28) and distinct, stretched or transverse mesh microsculpture.

Description. *Size.* SBL 7.8–8.7 mm, greatest width over elytra 2.8–3.2 mm. *Head.* Dorsal microsculpture not apparent at 50x magnification. Eyes small, flattened. Ocular ratio 1.26–1.31. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 28): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions absent, but with broad, very shallow depressions, outer basal impressions absent, rarely present as a shallow, poorly defined, broad depression, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 9 with 15 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color brunneous, macrosculpture distinct, dense irregularly punctulate, microsculpture not apparent at 50x magnification, luster moderately glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture very lightly

scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire. *Male* genitalia (Fig. 53): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract (Figs 75–76): apical margin of gonocoxite-1 with one seta, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 long, very slightly curved, narrowly rounded apex, bursa straight, relatively stout, cup-shaped, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa with short pouch, ventral modification of bursa absent.

Cerabilia (F.) uncata sp. nov.
(Figs 21, 49, 82)

Etymology. The specific epithet *uncata* is from the Latin for "hooked" and refers to the form of aedeagus tip. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "AUST:QLD:NE Mt Murray Prior, 8 Dec 1998 G.B. Monteith QM BELESATE 984, 16°56′S×145°51′E Rainforest, 770 m Sieved litter"//"QM Reg. No. T69249"//"EMEC1012173". QM.

Type locality. Queensland, northeast of Mt. Murray Prior, 16° 56'S 145° 51'E.

Diagnosis. Like *C. (F.) kalkajaka* above, this species has a prominently raised region of the anteroventral mesepisternum but is distinguished by its smaller size, darker piceous color and prominently depressed basolateral region of the pronotum (Fig. 21) that extends about a third of the pronotum length forward.

Description. *Size.* SBL 5.3–5.9 mm, greatest width over elytra 2.0–2.2 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, convex. Ocular ratio 1.25–1.38. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 21): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, broader across base than apex, lateral marginal bead well defined from apical angle to hind angle, basal margin straight, anterior margin medially broadly, shallowly emarginate, apical angles scarcely produced, hind angles obtusely rounded, anteriolateral setae very

near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 14 setigerous punctures, two setigerous punctures near apex of interval 7. Elytra: color rufopiceous or brunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster moderately glossy or glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed deeply, where impressed, impunctate. Metepisternum macrosculpture very lightly scabriculous, almost smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1–4 with lateral and medial sulci, 5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire. *Male* genitalia (Fig. 49): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and narrowly pointed, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view small ventral tooth or dorsal ridge, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract: female unknown.

Cerabilia (F.) wunduensis sp. nov.

(Figs 36, 85)

Etymology. The specific epithet *wunduensis* based on the eastern Kuku Yalanji Aboriginal people's name for the type locality Wundu (Thornton Peak) and is treated as an adjective.

Type material. HOLOTYPE, ♀. "N.E. Qld. Thornton Peak. 11 km N.E. Daintree. 1000–1200 m, 30 Oct - 1 Nov 1983, Monteith, Yeates & Thompson"//"QM Reg. No. T20049"//"EMEC1012136". QM.

Type locality. Queensland, Thorton Peak. Estimated coordinates 16° 10'S 145° 22'E.

Diagnosis. Small beetles with a compact, somewhat ovoid form. Smaller than the somewhat similar *C. (F.) spinifer*. Also darker piceous, with almost no trace of microsculpture.

Description. *Size.* SBL 4.6 mm, greatest width over elytra 1.8 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Eyes average size, somewhat flattened. Ocular ratio 1.09. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae, apical palpomeres glabrous. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth simple, blunt, triangular. Maxilla: apical palpomere glabrous, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 36): microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, widths all approximately equal, interval 9 with 14 setigerous punctures,

two setigerous punctures near apex of interval 7. Elytra: color rufopiceous, macrosculpture a few scattered small punctulae, microsculpture not apparent at 50x magnification, luster glossy. Humeri rounded or slightly angulate, without denticle. Elytral striae impressed moderately, where impressed, impunctate. Metepisternum macrosculpture smooth. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1 with lateral sulcus only, 2–3 with lateral and medial sulci, 4–5 without sulci. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire. Male genitalia: male unknown. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with one seta, lateral edge of gonocoxite-2 with two ensiform setae or with three ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, falcate, narrowly rounded apex, bursa very short, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermathecal gland duct connected at base of spermatheca, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Biliacera subgen. nov.

Type species. *Cerabilia Biliacera vitalis* sp. nov., (Fig. 7) here designated.

Characteristics. As for the genus and range of SBL 3.4–9.6 mm, greatest width over elytra 1.2–3.6 mm. Ocular ratio 1.04–1.37. Labial apical palpomeres plurisetose, with scattered short setae. Pronotum margins unisetose with posterolateral setae absent. Elytra with two setigerous punctures near apex of interval 7 and the third interval with one to five discal punctures. Humeri rounded or slightly angulate, without denticle.

Geographic Distribution. Found only in New Caledonia (Figs 143–146).

Cerabilia (Biliacera) aite sp. nov.
(Figs 107, 143)

Etymology. The specific epithet, treated as a Latinized noun in the nominative case, is from Até the Greek goddess of mischief, ruin, and folly. Até also refers to acts of hubris that leads to the downfall of a hero.

Type material. HOLOTYPE, ♀. "Table d'Union b.Col d'Amieu, Neu-Kaledonien", NMHW.

Type locality. Col d'Amieu Table Unio, estimated vicinity 21° 38'S 165° 49'E.

Diagnosis. Only *C. (B.) aite* and three other species (*C. (B.) discosetosa*, *C. (B.) edentata*, and *C. (B.) koghisensis*) have the anterior marginal seta of the pronotum positioned very far from the margin; 3–5x the width of the setal pore distant (Fig. 107). See diagnoses under those species.

Description. Size. SBL 6.5 mm, greatest width over elytra 3.0 mm. Head. Dorsal microsculpture visible as irregular mesh. Supra- and postorbital region smooth. Eyes small, flattened. Ocular ratio 1.25. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae. Glossal sclerite form truncate at apex, edge shelf-like, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth simple, acutely pointed, with single pair of fine setae paramedially near anterior margin. Paramedial pits deep, sharply defined, very small, diameter much less than 1/2 width between pits, paramedial pits glabrous. Maxilla: palpomere glabrous, penultimate palpomeres shorter than 2 and 4. Thorax. Pronotum (Fig. 107): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, overall shape transverse, greatest width slightly to significantly greater than length, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, broader across base than apex, lateral marginal bead well defined from apical angle to hind angle, basal

margin very shallowly emarginate in middle, anterior margin medially deeply, broadly emarginate, apical angles large, prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very distant from lateral margin, about 4x width of setal pore from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, widths all approximately equal, interval 3 with two setigerous punctures, 9 with 17. Elytra: color piceous, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster glossy. Elytral striae impressed deeply, impunctate. Prosternum smooth. Proepisternum smooth. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth. Mesosternum macrosculpture smooth or very lightly scabriculous. Metatarsomeres 1 with lateral sulcus only, 2–4 with lateral and medial sulci, 5 without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Metatrochanter form elongate, extended to half length of femur, rounded at apex, dorsally slightly flattened, fitted to sterna. Female protarsomeres 1–4 dorsally glabrous. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, apical margin entire, ventrites IV–VI glabrous. Male genitalia: male unknown. Female genitalia and reproductive tract: female type not dissected.

Cerabilia (B.) amieuensis sp. nov.
(Figs 101, 122, 144)

Etymology. The specific epithet *amieuensis* is based on the type locality Col d' Amieu and is treated as an adjective.

Type material. HOLOTYPE, ♂. "21°34'29"S/ 165°45'19"E, NEW CALEDONIA, Prov.Sud. Col d'Amieu, 510 m el., 16:iii:2007, coll. KWill, leaf litter, logs"//"EMEC61814". Source EMEC, MNHN.

Type locality. New Caledonia, Southern Province, Col d'Amieu, 21° 34'S 165° 45'E.

Diagnosis. This species is only known from a male specimen, which is very similar to *C. (B.) inversa* males except for the much larger profemur and more pronounce arcuate form of the hind tibia in the latter species. Male genitalia are distinctly different (Figs 122, 123).

Description. *Size.* SBL 4.1 mm, greatest width over elytra 1.8 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with two to several well marked sulci. Eyes average size, somewhat flattened. Ocular ratio 1.16. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, very small and blunt. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 101): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions present, linear, sharp, straight, outer basal impressions absent, shape of lateral margins convergent in basal half, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture, 9 with 15 setigerous punctures. Elytra: color rufopiceous, macrosculpture smooth, microsculpture sculpticells slightly transversely elongate, or somewhat irregular, forming mesh, luster moderately glossy. Elytral striae impressed moderately. Prosternum rugosissimus across entire apical half. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture smooth, or with rugosities just

at anterior edge. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire, ventrites IV–VI glabrous. Male genitalia (Fig. 122): orientation of median lobe of aedeagus in repose right side up, orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view blunt. Female genitalia and reproductive tract: female unknown.

Cerabilia (B.) apicesecta sp. nov.
(Figs 91, 115, 143)

Etymology. The specific epithet *apicesecta* is a compound Latin word for "pinked apically," in reference to the excavation at the aedeagal apex. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "NEW CALEDONIA Ningua, nr summit, 13 Nov 2001, G.B.Monteith, QM Berlesate 1052, 21°45'S×166°09E, Rainforest, 1300 m, Sieved litter"//"EMEC1012129". Source QM, MNHN. PARATYPE. Pic Ningua summit, G.Hunt Sep 1993, 1350 m, EMEC207008, ♂, CAS.

Type locality. New Caledonia, Southern Province. Pic Ningua, 21° 45'S 166° 9'E.

Diagnosis. Relatively large and more elongate form than other species with sulci above and behind the eyes. The pronotum (Fig. 91) converges basally and basal impressions are very shallow and slightly oblique as opposed to straight and linear in other, similar species.

Description. *Size.* SBL 5.5 mm, greatest width over elytra 2.5 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with numerous well marked sulci. Eyes small, prominently convex. Ocular ratio 1.22. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and few small scattered setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth very low, broad, almost absent. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 91): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions absent, but with broad, very shallow depressions, outer basal impressions present as a shallow, poorly defined, broad depression, shape of lateral margins convergent in basal half, lateral marginal bead well defined from apical angle to hind angle, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture, 9 with 15 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster moderately glossy. Elytral striae impressed moderately. Prosternum

rugosissimus across entire apical half. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture with medial transverse ridge or smooth. Mesotarsomeres 1 with lateral and medial sulci, 2–5 without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1 with lateral sulcus only, 2–5 without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally with fine, short, scattered setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire, ventrites IV–VI glabrous. *Male* genitalia (Fig. 115): orientation of median lobe of aedeagus in repose right side up, orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broad, widening to apex, apex of median lobe in lateral view thick and reflexed ventrally, apex of median lobe in dorsal view broad and pinked medially. Female genitalia and reproductive tract: female unknown.

Cerabilia (B.) discosetosa sp. nov.
(Figs 6, 104, 125, 135, 146)

Etymology. The specific epithet *discosetosa* refers to the pronotal setae, which are positioned far from the margin, on the lower edge of the disc. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "22°09'00"S/ 166°41'12"E, NEW CALEDONIA, Prov.Sud. Riviére Bleue Pk, Houp Géant trail, 330 m el., 13:iii:2007. coll. KWill headlamp search"//"EMEC61769". Source EMEC, deposited MNHN. Same data as holotype with EMEC61771, NC1, kww435, ♂, EMEC and EMEC61770, ♀, EMEC.

Type locality. New Caledonia, Southern Province, Riviére Bleue Park, 22° 9'S 166° 41'E.

Diagnosis. Only *C. (B.) discosetosa* and three other species (*C. (B.) edentata*, *C. (B.) koghisensis*, and *C. (B.) aite*) have the anterior marginal seta of the pronotum positioned very far from the margin; 3–5x the width of the setal pore distant (Fig. 104). *Cerabilia Biliacera discosetosa* is easily separated from the other three species by having four to five setigerous punctures on elytral interval 3, compared to one (rarely two) in the other species and its relatively large size (Fig. 6).

Description. *Size.* SBL 7.6–9.0 mm, greatest width over elytra 2.9–3.3 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes average size, somewhat flattened. Ocular ratio 1.29–1.37. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 pubescent in apical 1/3–1/2. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form truncate at apex, edge shelf-like, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Paramedial pits deep, sharply defined, very small, diameter much less than 1/2 width between pits, paramedial pits glabrous. Maxilla: antepenultimate palpomere glabrous or with 1–2 small apical setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 104): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin with medial third quadrate emarginate, anterior margin medially deeply, broadly emarginate, apical angles large, prominent, hind angles obtusely rounded, anteriolateral setae very distant from lateral margin, about 3x width of setal pore from lateral margin. Elytron with nine intervals, form of intervals

convex in apical third, nearly flat in basal third, interval 3 with four setigerous punctures, rarely with five setigerous punctures, 9 with 15 setigerous punctures. Elytra: color rufopiceous, microsculpture not apparent at 50x magnification, luster glossy. Elytral striae impressed deeply or moderately. Prosternum smooth or slightly, irregularly rugulose. Proepisternum smooth or slightly, irregularly rugulose. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1 with lateral sulcus only, 2–4 with lateral and medial sulci, 5 without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally with fine, short, scattered setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia (Fig. 125): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view arcuate, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract (Fig. 135): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 moderately long, slightly curved, broadly rounded apex, bursa short, left directed, common oviduct inserted near apex, right lateral portion of bursa with very large pouch, base broadly joined to bursa, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct with notable expanded region near base of gland, gland form elongate, rounded and slightly expanded apically, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) dominatrix sp. nov.
(Figs 111, 130, 145)

Etymology. The specific epithet is based on *dominatrix*, Latin for a female ruler, and is treated as a noun in the nominative singular standing in apposition.

Type material. Holotype, ♂. "NEW CALEDONIA, 11097, 21°53'S×166°25'E, 1600 m Mt Humboldt summit, 5 Nov 2002, Monteith & Burwell, pyreth, trees & logs, H/19"//"EMEC1012126". Source QM, deposited MNHN.

Type locality. New Caledonia, Mt. Humboldt summit, 21° 52'S 166° 25'E.

Diagnosis. Very large beetles. In New Caledonia only *C. (B.) francisca* approaches the same size. These two are readily separated by the narrow, rounded form of the pronotum, with broad, flat regions laterad of the basal impressions in *C. (B.) dominatrix* (Fig. 111) compared to the low convexity separating the impressions from the margin in *C. (B.) francisca* (Fig. 110). The dorsal surface of the pronotum in *C. (B.) dominatrix* is smooth and in *C. (B.) francisca* it has distinct, irregular, scattered micropunctulae.

Description. *Size.* SBL 9.6 mm, greatest width over elytra 3.3 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes average size, somewhat flattened. Ocular ratio 1.30. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal

base, antennomere 3 pubescent in apical 1/3–1/2. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth simple, blunt, triangular. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 111): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions present as a broad, deep, poorly defined depression that is continuous with broad flat area and reflex at hind angles, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to slightly beyond hind angle and onto base, basal margin straight, anterior margin medially broadly, shallowly emarginate, apical angles scarcely produced, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex, interval 3 with three setigerous punctures, 9 with 16 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Elytral striae impressed deeply or moderately. Prosternum smooth. Proepisternum smooth. Metepisternum macrosculpture very lightly scabriculous, almost smooth. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire, ventrites IV–VI glabrous. Male genitalia (Fig. 130): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view blunt. Female genitalia and reproductive tract: female unknown.

Cerabilia (B.) drupa sp. nov.

(Figs 98, 139, 143)

Etymology. The specific epithet *drupa*, Latin for a wrinkled olive, refers to the ventral rugosities on the body of these beetles, and is treated as a noun in the nominative singular standing in apposition.

Type material. HOLOTYPE, ♀. "NEW CALEDONIA Mandjelia, 12 May 1984, G.Monteith & D.Cook, Q.M. BERLESATE No. 646, 20.45S × 164.32E, Rainforest, 700 m Litter"//" EMEC1012133". Source QM, deposited MNHN. PARATYPE. Mandjelia, 580 m, lower creek 11–12Dec2004, Rainforest, 11950 G.Monteith, dung trap, EMEC1012134, ♀, QM.

Type locality. New Caledonia, Northern Province, Mandjelia, 20° 24'S 164° 32'E.

Diagnosis. Distinctively elongate body form, smoothly arcuate shape of the pronotum, and mentum with small pits, distinguish this species from others any of the other medium or small sized beetles in the subgenus

Description. *Size.* SBL 4.7 mm, greatest width over elytra 1.5 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with two to several well marked sulci. Eyes average size, somewhat flattened. Ocular ratio 1.19–1.21. Antennae: overall length moderately long, with antennomere 11 just

reaching beyond pronotal base, antennomere 3 pubescent in apical 1/3–1/2. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Paramedial pits deep, sharply defined, very small, diameter much less than 1/2 width between pits, paramedial pits glabrous. Maxilla: antepenultimate palpomere glabrous or with 1–2 small apical setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax*. Pronotum (Fig. 98): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin straight, anterior margin medially broadly, shallowly emarginate, apical angles scarcely produced, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex, interval 3 with one setigerous puncture, 9 with 16 setigerous punctures. Elytra: color brunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells slightly transversely elongate, or somewhat irregular, forming mesh, luster moderately glossy. Elytral striae impressed moderately. Prosternum rugosissimus laterally, irregularly rugulose or smooth anteromedially. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatarsomeres 1 with lateral sulcus only, 2–5 without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen*. Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia: male unknown. Female genitalia and reproductive tract (Fig. 139): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa straight elongate, common oviduct inserted in apical cup, right lateral portion of bursa with very large pouch, narrow at base, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, gland duct length moderately elongate, gland duct diameter increasing apically, without notable expansion, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) edentata sp. nov.
(Figs 105, 126, 136, 145)

Etymology. The specific epithet *edentata* derived from the Latin, "to be without teeth" and refers to the absence of the mentum tooth in this species. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "22°09'00"S/ 166°41'12"E, NEW CALEDONIA, Prov.Sud. Riviére Bleue Pk, Houp Géant trail, 330 m el.,13:iii:2007. coll. KWill, headlamp search"//"EMEC61772". Source EMEC, deposited MNHN. PARATYPES. Same data as holotype with EMEC61775, ♀, EMEC; EMEC61777, EMEC617783 NC2 kww436, EMEC61774, 3♂♂, EMEC; EMEC61773, ♂, QM; EMEC61776, ♀, QM.

Type locality. New Caledonia, Southern Province, Riviére Bleue Park, 22° 9'S 166° 41'E.

Diagnosis. Only *C. (B.) edentata* and three other species (*C. (B.) discosetosa*, *C. (B.) koghisensis*, and *C. (B.) aite*) have the anterior marginal seta of the pronotum positioned very far from the margin; 3–5x the width of the setal pore distant (Fig. 105). *Cerabilia Biliacera edentata* is easily separated from the other three species

by its small size and the absence of the mentum tooth.

Description. *Size.* SBL 4.4–6.0 mm, greatest width over elytra 1.7–2.1 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes average size, somewhat flattened. Ocular ratio 1.21–1.26. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and few small scattered setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth absent. Paramedial pits deep, sharply defined, very small, diameter much less than 1/2 width between pits, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 105): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions present, linear, sharp, slightly divergent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very distant from lateral margin, about 3x width of setal pore from lateral margin. Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Elytral striae impressed moderately. Prosternum smooth. Proepisternum smooth. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–2 with lateral and medial sulci, 3–5 without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1 with lateral sulcus only, 2–4 with lateral and medial sulci, 5 without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally with fine, short, scattered setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia (Fig. 126): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view narrowly rounded point. Female genitalia and reproductive tract (Fig. 136): apical margin of gonocoxite-1 with one seta or with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa straight elongate, common oviduct inserted in apical cup, right lateral portion of bursa not differentially developed, dorsal development of bursa large pouch, spermatheca not evident, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected to common oviduct, gland duct length short, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) espee sp. nov.
(Figs 9, 108, 128, 144)

Etymology. The specific epithet "espee" is arbitrary combination of letters treated as a noun in apposition.

Type material. HOLOTYPE, ♂. "NEW CALEDONIA, 11131, 21°53'S×166°25'E.1350 m Mt Humboldt, refuge. Night collecting. 5–8 Nov 2002 Burwell, Monteith & Wright"//"EMEC1012117". Source QM, deposited MNHN. PARATYPES. Mt. Humboldt refuge. 7–8 Nov 2002 G.Monteith & S.Wright, QM Berlesate 1076, 21°53'S 166°25'E. rainforest, 1300 m sifted litter, EMEC1012120 and same with EMEC1012118, 2♀♀, QM; EMEC1012119, ♂, QM.

Type locality. New Caledonia, Southern Province, Mt. Humboldt, 21° 53'S 166° 25'E.

Diagnosis. Similar to *C. (B.) neocaledonica* but with relatively smaller and more quadrate pronotum (Fig. 108) and more elongate-ovoid elytral form (Fig. 9).

Description. *Size.* SBL 5.4–5.7 mm, greatest width over elytra 2.1–2.3 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes average size, somewhat flattened. Ocular ratio 1.23–1.26. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and few small scattered setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth simple, acutely pointed. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum: microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, macrosculpture smooth, inner basal impressions present, linear, sharp, straight, outer basal impressions present as a shallow, poorly defined, broad depression, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to slightly beyond hind angle and onto base, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals convex in apical third, nearly flat in basal third, interval 3 with one setigerous puncture, 9 with 16 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster glossy. Elytral striae impressed deeply or moderately. Prosternum smooth. Proepisternum smooth. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1 with lateral and medial sulci, 2–5 without sulci. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Female protarsomeres 1–4 dorsally with fine, short, sparse, scattered setae, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia (Fig. 128): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view thick and reflexed ventrally, apex of median lobe in dorsal view

blunt. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 long, very slightly curved, narrowly rounded apex, bursa straight elongate, common oviduct inserted in apical cup, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at posterior oriented apex, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) francisca sp. nov.
(Figs 110, 129, 137, 145)

Etymology. The specific epithet *francisca* is an allusion to a throwing axe used by the Franks in the Middle Ages and draws attention to the shape of the aedeagus tip, which is shaped like a Frankish throwing axe. It is treated as a noun in the nominative singular standing in apposition.

Type material. Holotype, ♂. "22°10′28"S/166°30′48"E NEW CALEDONIA, Prov. Sud. Mt. Koghis, 700 m el.coll. KWill 12:iii:2007, headlamp search"/ /"EMEC61786". Source EMEC, deposited MNHN. PARATYPE. Same data as holotype with EMEC61787 NC13 kww439, ♂, EMEC.

Type locality. New Caledonia, Southern Province, Mt. Koghis, -22.1744; 166.5133 22° 10'S 166° 30'E.

Diagnosis. Large sized beetles. In New Caledonia only *C. (B.) dominatrix* approaches the same size. See diagnosis under *C. (B.) dominatrix*.

Description. *Size.* SBL 9.1–10.0 mm, greatest width over elytra 3.6 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes small, flattened. Ocular ratio 1.30. Antennae: overall length short, not reaching base of pronotum, antennomere 3 pubescent in apical 1/3–1/2. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form truncate at apex, edge shelf-like, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Paramedial pits deep, well defined, large, diameter greater than 1/2 width between pits, elongate, prolonged anterad, paramedial pits with numerous (about 7–12) setae on lateral face extended medially. Maxilla: antepenultimate palpomere glabrous or with 1–2 small apical setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 length subequal. *Thorax.* Pronotum (Fig. 110): microsculpture not or scarcely apparent at 50x magnification, macrosculpture with very fine, scattered micropunctulae, inner basal impressions present, short, shallow, broad, not well delimited, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to beyond hind angle and onto base nearly to inner impression, wider in basal 1/4, basal margin straight, anterior margin medially broadly, shallowly emarginate, apical angles scarcely produced, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with ten intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with two setigerous punctures or with three setigerous punctures, 9 with 16 setigerous punctures. Elytra: color rufopiceous, macrosculpture irregular mix of slightly larger and many smaller punctulae, microsculpture not apparent at 50x magnification, luster glossy. Elytral striae impressed moderately. Prosternum slightly, irregularly rugulose. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly,

shallowly arcuate. Metatarsomeres 1 with lateral sulcus only, 2–5 without sulci. Dorsal surface of meso- and metatarsomeres setose. Male protarsomeres 1–3 dorsally pubescent, with numerous long setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally pubescent, with long scattered setae, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia (Fig. 129): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view arcuate, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view blunt. Female genitalia and reproductive tract (Fig.137): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 glabrous, gonocoxite-2 short, falcate, narrowly rounded apex, bursa long, left directed curved form, common oviduct inserted near apex, right lateral portion of bursa with very large pouch, narrow at base, dorsal development of bursa lacking, spermatheca very short sessile, sclerotized, plaquiform, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at posterior oriented apex, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate, rounded and slightly expanded apically, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) inversa sp. nov.
(Figs 102, 123, 134, 145)

Etymology. The specific epithet *inversa* from the Latin *inverto*, "to be upside down" and this refers to the reversed orientation of the aedeagus when in repose. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. " NEW CALEDONIA, Col d'Amieu, 55 m 15 Oct 1978 G.Kuschel"//"Sifted litter and rotten wood 78/229"//"EMEC201499". NZAC. PARATYPES. Table Unio road, 600 m 14 Nov 2000, Bouchard. Burwell & Monteith, 9934, EMEC61816, ♀, EMEC. Col d'Amieu, 440 m el., 16:iii:2007, headlamp search, K.Will, EMEC61817, ♀, EMEC. Sud. Col d' Amieu, 485 m el., 14:iii:2007 coll. KWill, ex leaflitter, kww440, NC18, EMEC61815, ♂, EMEC. Table Unio,900 m nr col d'Amieu, 16 Oct 1978 G.Kuschel, Sifted litter and rotten wood, 78/234, EMEC201494, ♀, NZAC. Table Unio, 800 m nr col d'Amieu 16 Oct 1978, G.Kuschel, Sifted litter and rotten wood 78/235, EMEC201497, ♀, NZAC. Col d'Amieu. 440 m 26 May 1987 R.Raven, Handsorted litter, EMEC1012128, ♂, QM.

Type locality. New Caledonia, Southern Province, Col d'Amieu. Estimated coordinates: 21° 32' S 165° 45'E.

Diagnosis. Very similar to and sympatric with *C. (B.) amieuensis*. Distinguished from that species by the form of the male genitalia (Fig. 123) and features discussed under that species above.

Description. *Size.* SBL 5.0–5.1 mm, greatest width over elytra 1.9–2.0 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with two to several well marked sulci. Eyes average size, somewhat flattened. Ocular ratio 1.22–1.24. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, very small and blunt. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 102): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner

basal impressions present, linear, sharp, straight, outer basal impressions absent, shape of lateral margins convergent in basal half, lateral marginal bead well defined from apical angle to hind angle, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture, 9 with 15 setigerous punctures. Elytra: color brunneous, macrosculpture smooth, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster moderately glossy. Elytral striae impressed moderately. Prosternum rugosissimus across entire apical half. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1 with lateral and medial sulci, 2–5 without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin obtusely angulate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia (Fig. 123): orientation of median lobe of aedeagus in repose right side up, orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broad, widening to apex, apex of median lobe in lateral view thick margin rounded not flexed, apex of median lobe in dorsal view broad and emarginate. Female genitalia and reproductive tract (Fig. 134): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, bluntly rounded apex, bursa straight elongate, common oviduct inserted in apical cup, right lateral portion of bursa with very large pouch, narrow at base, dorsal development of bursa lacking, spermatheca very short sessile, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at posterior oriented apex, gland duct length short, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) kanakorum sp. nov.

(Figs 95, 133, 143)

Etymology. The specific epithet *kanakorum* is treated as a noun in the genitive case and honors the Kanak people of New Caledonia, where this species is endemic.

Type material. HOLOTYPE, ♀. "NEW CALEDONIA, 12264, 22°11'S × 166°31'E, Mt Koghis, track entrance, 6 May 2005. 500 m, G.B.Monteith, berlesate"/ /"EMEC1012122". Source QM, deposited MNHN. PARATYPE. Mt. Dzumac road, 31 Oct 2001, G.B.Monteith, QM Berlesate 1059 Rainforest, 700 m Sieved litter, EMEC1012123 NC8 kww525, ♀, QM.

Type locality. New Caledonia, Southern Province, Mt. Koghis, 22° 11'S 166° 31'E.

Diagnosis. This species is very similar to *C. rubrica* and can be distinguished by the pronotal form as stated in the key and male genitalia. The pronotum is proportionally much smaller with less arcuate margins in *C. (B.) kanakorum*.

Description. *Size.* SBL 4.7–5.1 mm, greatest width over elytra 1.8–2.0 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes small, flattened. Ocular ratio 1.04–

1.16. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, acutely pointed. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum: microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, macrosculpture smooth, inner basal impressions present, linear, sharp, slightly convergent, outer basal impressions present as a shallow, poorly defined, broad depression, shape of lateral margins convergent in basal half, lateral marginal bead well defined from apical angle to hind angle or to slightly beyond hind angle and onto base, widening in basal third, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, interval 3 with one setigerous puncture, 9 with 16 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Elytral striae impressed moderately. Prosternum smooth. Proepisternum smooth. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia: male unknown. Female genitalia and reproductive tract: apical margin of gonocoxite-1 glabrous or with one seta, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, falcate, narrowly rounded apex, bursa long, right directed curved form, common oviduct inserted near apex, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not (Figs) apex, gland duct length very elongate, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) klingonorum sp. nov.
(Figs 8, 92, 116, 143, 148)

Etymology. The specific epithet "klingonorum" is a Latinized word that alludes to the deep head wrinkles in this species, reminiscent of the cranial structures of the Klingons of the Star Trek universe (Roddenberry 1979).

Type material. Holotype, ♂. "21°35'06"S 165°48'56"E NEW CALEDONIA, Prov. Sud. E of Table Unio, RP5 (rd from Sarraméa to Canala), 310 m el. 17:iii:2007, coll. K.Will headlamp search, leaf litter"//"EMEC61781". Source EMEC, deposited MNHN. PARATYPES. Same data as holotype with EMEC61782 and EMEC61785 NC12 kww438, 2♂♂, EMEC; EMEC61783, ♀, EMEC; EMEC61784, ♂, QM.

Type locality. New Caledonia, Southern Province, Table Unio, 21° 36'S 165° 49'E.

Diagnosis. Compared to other species with rugose heads such as *C. (B.) apicesecta* and *C. (B.) vitalis*, these beetles combine three or more sulci behind the eye (Fig. 148), tooth of mentum

triangular, and glabrous sternites. Very similar in all external characteristics (Fig. 8) to the slightly smaller *C. (B.) vitalis*. Male genitalia are decisively different, however (Fig. 116).

Description. *Size.* SBL 4.8–5.5 mm, greatest width over elytra 2.0–2.1 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with numerous well marked sulci. Eyes small, prominently convex. Ocular ratio 1.17–1.25. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and few small scattered setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 92): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture with very fine, scattered micropunctulae, inner basal impressions present, shallow, but defined medially, not delimited laterally, blending into broad depression, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles nearly right angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, interval 3 with one setigerous puncture, 9 with 15 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, luster moderately glossy. Elytral striae impressed moderately. Prosternum rugosissimus across entire apical half. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture rugulose in anterior third. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. *Male* genitalia (Fig. 116): orientation of median lobe of aedeagus in repose right side up, orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view arcuate, blade of median lobe in ventral view base with broad lobe on right side, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 glabrous or with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa right side significantly longer than left, overall relatively stout, cup-shaped, right lateral portion of bursa with very large pouch, narrow at base, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct,

spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) koghisensis sp. nov.
(Figs 106, 127, 144)

Etymology. The specific epithet *koghisensis* is based on the type locality Mt. Koghis and is treated as an adjective.

Type material. HOLOTYPE, ♂. "NEW CALEDONIA, Mt Koghis, 3 Nov 2002, G.Monteith. QM Berlesate 1072, 22°11'S 166°01'E, Rainforest, 700 m sieved litter, H/20"//"EMEC1012125". Source QM, deposited MNHN. PARATYPES. Mt Koghis, 735 m, 9 Oct 1978, G.Kuschel, Sifted leaf litter 78/217, EMEC201495, ♂, NZAC. Monts Koghis, forest litter, ca. 5 km N Nouméa, 550 m, 25.XI.2009, Schuh (11A), EMEC201496, ♂, NMHW.

Type locality. New Caledonia, Southern Province, Mt. Koghis, 22° 11'S 166° 31'E.

Diagnosis. Only *C. (B.) koghisensis* and three other species (*C. (B.) discosetosa*, *C. (B.) edentata*, and *C. (B.) aite*) have the anterior marginal seta of the pronotum positioned very far from the margin; 3–5x the width of the setal pore distant (Fig. 106). See diagnoses under *C. discosetosa* and *C. (B.) edentata* for distinguishing those species. *Cerabilia Biliacera koghisensis is* most similar to *C. (B.) aite*, differing in the proportions and shape of the pronotum and elytra. *Cerabilia Biliacera koghisensis* has a deeply emarginate pronotal basal margin (Fig. 106) and the elytra are somewhat elongate ovoid. *Cerabilia Biliacera aite* has a nearly straight pronotal basal margin (Fig. 107) and the elytra are somewhat stoutly ovoid.

Description. *Size.* SBL 6.7 mm, greatest width over elytra 1.5 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes small, flattened. Ocular ratio 1.28. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 pubescent in apical 1/3–1/2. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and few small scattered setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, acutely pointed. Paramedial pits deep, sharply defined, very small, diameter much less than 1/2 width between pits, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig 106): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions absent, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin smoothly, moderately emarginate in middle, anterior margin medially deeply, broadly emarginate, apical angles large, prominent, hind angles obtusely rounded, anteriolateral setae very distant from lateral margin, about 4.5x width of setal pore from lateral margin. Elytron with nine intervals, form of intervals convex in apical third, nearly flat in basal third, interval 3 with one setigerous puncture, 9 with 16 or 17 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Elytral striae impressed deeply or moderately. Prosternum smooth. Proepisternum smooth. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin obtusely angulate. Metatarsomeres 1 with lateral sulcus only, 2–4 with lateral and medial sulci, 5 without sulci. Dorsal surface of meso- and

metatarsomeres glabrous. Male protarsomeres 1–3 dorsally with fine, short, scattered setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire, ventrites IV–VI glabrous. Male genitalia (Fig. 127): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract: female unknown.

Cerabilia (B.) letalis sp. nov.
(Figs 97, 120, 145)

Etymology. The specific epithet *letalis* is from the Latin for "deadly" and is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "21°37'14"S 165°52'16"E, NEW CALEDONIA, Prov. Sud. trail to Plateau de Dogny, 725–900 m, 15:iii:2007, coll. K.Will headlamp search, leaf litter"//"EMEC61806". Source EMEC, deposited MNHN. PARATYPES. Same data as holotype with EMEC61808, EMEC61809; EMEC61810; EMEC61811; EMEC61813, 5♂♂, EMEC; EMEC61812 NC16 kww444, ♀, EMEC; EMEC61807, ♂, QM.

Type locality. New Caledonia, Southern Province, trail to Plateau de Dogny, 21° 37'S 165° 52'E.

Diagnosis. Very similar to *C. (B.) vitalis*, with which it is sympatric, but consistently smaller and with a notably smoother prosternum and usually smoother in other areas of the ventral surface.

Description. *Size.* SBL 3.5–3.8 mm, greatest width over elytra 1.4–1.5 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with two to several well marked sulci. Eyes small, flattened. Ocular ratio 1.17–1.21. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth simple, very small and blunt. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 97): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions present, linear, sharp, slightly convergent, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture, 9 with 15 setigerous punctures. Elytra: color rufopiceous, macrosculpture a few scattered small punctulae, microsculpture sculpticells slightly transversely elongate, or somewhat irregular, forming mesh, luster moderately glossy. Elytral striae impressed moderately. Prosternum rugosissimus laterally, irregularly rugulose or smooth anteromedially. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture rugulose in anterior third. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface

of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia (Fig. 120): orientation of median lobe of aedeagus in repose right side up, orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view arcuate and curved ventrally, blade of median lobe in ventral view broad, widening to apex, apex of median lobe in lateral view thick and reflexed ventrally, apex of median lobe in dorsal view broad and emarginate. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with one seta or with two setae, lateral edge of gonocoxite-2 with one ensiform seta or with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, falcate, narrowly rounded apex, bursa straight, relatively stout, cup-shaped, right lateral portion of bursa with very large pouch, narrow at base, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at posterior oriented apex, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) mouensis sp. nov.
(Figs 94, 118, 143)

Etymology. The specific epithet *mouensis* is based on the type locality Mt. Mou and is treated as an adjective.

Type material. HOLOTYPE, ♂. "NEW CALEDONIA Mt Mou summit, 1200 m, 24 May 1984, G.Monteith & D.Cook"//"EMEC1012116". Source QM, deposited MNHN.

Type locality. New Caledonia, Southern Province, Mt. Mou. Estimated coordinates: 22° 3'S 166° 21'E.

Diagnosis. In combination, the smooth region above and behind the eyes, lack of sulci on the mesotarsomeres, and single elytral puncture in interval 3 separates this species from similar, if slightly smaller species such as *C. (B.) letalis* and *C. (B.) vitalis*.

Description. *Size.* SBL 6.3 mm, greatest width over elytra 2.3 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes average size, somewhat flattened. Ocular ratio 1.24. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 94): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions present, linear, sharp, straight, outer basal impressions present as a shallow, poorly defined, broad depression, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval

3 with one setigerous puncture, 9 with 16 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Elytral striae impressed moderately. Prosternum smooth. Proepisternum smooth. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally with fine, short, scattered setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire, ventrites IV–VI glabrous. *Male* genitalia (Fig. 118): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller with rounded point, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view thick and reflexed ventrally, apex of median lobe in dorsal view blunt. Female genitalia and reproductive tract: female unknown.

Cerabilia (B.) nana sp. nov.
(Figs 114, 132, 146)

Etymology. The specific epithet *nana* is a Latin adjective meaning dwarf and it alludes to the small size of these beetles. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "NEW CALEDONIA, 9913, 22°03'S 166°28'E, Mt Dzumac road, 700 m 1 Dec 2000., GB Monteith, Pyrethrum, trunks & logs"//"EMEC1012132". Source QM, deposited MNHN.

Type locality. New Caledonia, Southern Province, Mt. Dzumac road, 22° 3'S 166° 28'E.

Diagnosis. Smallest beetles, similar to *C. (B.) orbiculata* in having a broad bead of the lateral margin of the pronotum (Fig. 114) that widens basally, while in *C. (B.) nana*, it is narrower and less convex.

Description. *Size.* SBL 3.4 mm, greatest width over elytra 1.5 mm. *Head.* Dorsal microsculpture with sculpticells transversely elongate, longitudinally short relative to body axis. Supra- and postorbital region with two to several well marked sulci. Eyes average size, somewhat flattened. Ocular ratio 1.20. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth simple, acutely pointed. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 114): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions present, linear, sharp, slightly divergent, outer basal impressions absent, shape of lateral margins convergent in basal half, lateral marginal bead well defined from apical angle to beyond hind angle and onto base nearly to inner impression, wider in basal 1/4, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin.

Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture, 9 with 15 setigerous punctures. Elytra: color rufopiceous, macrosculpture smooth, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster moderately glossy. Elytral striae impressed moderately. Prosternum rugosissimus laterally, irregularly rugulose or smooth anteromedially. Proepisternum rugosissimus. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture rugulose or scabriculous. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire, ventrites IV–VI glabrous. Male genitalia (Fig. 132): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract: female unknown.

Cerabilia (B.) neocaledonica sp. nov.
(Figs 109, 143)

Etymology. The specific epithet *neocaledonica* is based on this species' occurrence in New Caledonia and is treated as an adjective.

Type material. HOLOTYPE, ♀. "NEW CALEDONIA, 11787, 22°15'S×166°49'E, 280 m, Pic du Pin, site 1, rainfor. 26 Nov 2004, berlesate, G.Monteith, P.Grimbacher" //"Photog. Spm. PS0260"//"EMEC1012124". Source QM, deposited MNHN.

Type locality. New Caledonia, Southern Province, Pic du Pin, 22° 15'S 166° 49'E.

Diagnosis. Similar to *C. (B.) espee* but with a relatively larger pronotum (Fig. 109) that has more arcuate lateral margins, and more ovoid elytral form.

Description. *Size.* SBL 7.1 mm, greatest width over elytra 2.6 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes average size, convex. Ocular ratio 1.33. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 pubescent in apical 1/3–1/2. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form apex medially, slightly emarginate, edge thin. Mentum anterior margin moderately emarginate, tooth simple, acutely pointed. Paramedial pits deep, sharply defined, very small, diameter much less than 1/2 width between pits, paramedial pits glabrous. Maxilla: antepenultimate palpomere glabrous or with 1–2 small apical setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 109): microsculpture not or scarcely apparent at 50x magnification, macrosculpture with very fine, scattered micropunctulae, inner basal impressions absent, but with broad, very shallow depressions, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to slightly beyond hind angle and onto base, basal margin straight, anterior margin medially broadly, shallowly emarginate, apical angles scarcely produced, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals

flat, slightly more convex near apex, interval 3 with three setigerous punctures, 9 with 16 or 17 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture not apparent at 50x magnification, luster glossy. Elytral striae impressed moderately. Prosternum smooth. Proepisternum slightly, irregularly rugulose. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres 1–3 with lateral and medial sulci, 4–5 without sulci. Metatarsomeres 1 with lateral sulcus only, 2–4 with lateral and medial sulci, 5 without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Female protarsomeres 1–4 dorsally with fine, short, sparse, scattered setae, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia: male unknown. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, falcate, narrowly rounded apex, bursa straight elongate, common oviduct inserted near apex, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length moderately elongate, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) orbiculata sp. nov.
(Figs 113, 141–142, 146)

Etymology. The specific epithet *orbiculata* is Latin for "rounded shape" and draws attention to the overall form of these beetles. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♀. "NEW CALEDONIA, 11150, 22°01'S 166°28E Mt Ouin, 1100 m. 9 Nov 2002, C.Burwell & G.Monteith, pyrethrum, trees & logs, H/21"//"EMEC1012130//"NC23 kww530. Source QM, deposited MNHN.

Type locality. New Caledonia, Southern Province, Mt. Ouin, 22° 1'S 166° 28'E.

Diagnosis. Larger, more convex and ovoid than *C. (B.) nana* that it otherwise resembles.

Description. *Size.* SBL 4.0 mm, greatest width over elytra 1.4 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with two to several well marked sulci. Eyes small, flattened. Ocular ratio 1.27. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth simple, acutely pointed. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 113): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture with very fine, scattered micropunctulae, inner basal impressions present, linear, sharp, straight, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, lateral marginal bead well defined from apical angle to slightly beyond hind angle and onto base to level of inner impression, basal margin straight, anterior margin medially broadly, shallowly emarginate, apical angles scarcely produced, hind angles obtusely angled, rounded not sharp,

anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex, interval 3 with one setigerous puncture, 9 with 15 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster glossy. Elytral striae impressed moderately. Prosternum rugosissimus laterally, irregularly rugulose or smooth anteromedially. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatarsomeres 1 with lateral sulcus only, 2–5 without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia: male unknown. Female genitalia and reproductive tract (Fig. 141–142): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 short, falcate, narrowly rounded apex, bursa right side significantly longer than left, overall relatively stout, cup-shaped, right lateral portion of bursa with very large pouch, narrow at base, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at posterior oriented apex, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) paniensis sp. nov.
(Figs 100, 142, 143)

Etymology. The specific epithet *paniensis* is based on the type locality, Mt. Panie, and is treated as an adjective.

Type material. HOLOTYPE, ♀. "NEW CALEDONIA Mt Panié 16 May 1984, G.Monteith & D.Cook, QM BERLESATE No. 650, 20.35S×164.47E, Rainforest, 900 m Litter"//"EMEC1012131". Source QM, deposited MNHN.

Type locality. New Caledonia, Northern Province, Mt. Panie, 20° 35'S 164° 47'.

Diagnosis. The smallest beetles of those species with sulci above the eye. Additionally distinguished by the pubescence on the apical half of antennomere 3.

Description. *Size.* SBL 3.8 mm, greatest width over elytra 1.5 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with two to several well marked sulci. Eyes average size, somewhat flattened. Ocular ratio 1.27. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 pubescent in apical 1/2. Labral apical margin with four setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth simple, very small and blunt. Paramedial pits deep, sharply defined, very small, diameter much less than 1/2 width between pits, paramedial pits glabrous. Maxilla: antepenultimate palpomere glabrous or with 1–2 small apical setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 100): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions present as a broad, deep, poorly defined depression that is continuous with broad flat area and reflex at hind angles, outer basal impressions absent, shape of lateral margins smoothly, moderately

arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, interval 3 with one setigerous puncture, 9 with 14 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster glossy. Elytral striae impressed moderately. Prosternum rugosissimus across entire apical half. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally glabrous. Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of female with two pairs setae, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia: male unknown. Female genitalia and reproductive tract (Fig. 142): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa straight, relatively stout, cup-shaped, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) rubrica sp. nov.
(Figs 96, 119, 144)

Etymology. The specific epithet *rubrica* is from the Latin for red ochre and refers to the color of the soil in the area in which this species. It is treated as a noun in the genitive case.

Type material. HOLOTYPE, ♂. "NEW CALEDONIA, R. Bleu, main forest. 17 Nov 2001, G.B. Monteith, QM Berlesate 1047, 22°06'S x 166°40'E, Rainforest, 160 m, Sieved litter"//"EMEC1012121". Source QM, deposited MNHN. PARATYPES. Riviére Bleue Pk, Houp Géant trail 330 m el.,13:iii:2007. coll. KWill headlamp search, EMEC61779, ♀, EMEC; same data with EMEC61780 NC5 kww437, ♂, EMEC.

Type locality. New Caledonia, Southern Province, Riviére Bleue Park, 22° 6'S 166° 40'E.

Diagnosis. Similar to *C. (B.) kanakorum* but can be distinguished by the pronotal form (Fig. 96) (the pronotum is proportionally much larger with more arcuate margins in *C. (B.) rubrica)* and male genitalia (Fig. 119).

Description. *Size.* SBL 4.5–5.1 mm, greatest width over elytra 1.9–2.0 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region smooth or with slight depressed areas around setae. Eyes average size, somewhat flattened. Ocular ratio 1.27–1.33. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin shallowly emarginate, tooth simple, acutely pointed. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 96): microsculpture not or scarcely apparent at 50x magnification, macrosculpture smooth, inner basal impressions present, linear, sharp,

straight, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to slightly beyond hind angle and onto base, widening in basal third, basal margin smoothly, moderately emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture, 9 with 16 setigerous punctures. Elytra: macrosculpture a few scattered small punctulae, microsculpture not apparent at 50x magnification, luster glossy. Elytral striae impressed moderately. Prosternum smooth. Proepisternum smooth. Metepisternum macrosculpture rugulose or lightly scabriculous. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture smooth or very lightly scabriculous. Tarsomere 5 on all legs ventrally glabrous, rarely ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia (Fig. 119): orientation of median lobe of aedeagus in repose left side up, orientation of ostium dorsal, form of left paramere conchoid, larger, right smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with one seta or with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 moderately long, slightly curved, broadly rounded apex, bursa straight elongate, common oviduct inserted near apex, right lateral portion of bursa not differentially developed, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) ruginosa sp. nov.
(Figs 112, 131, 140, 145)

Etymology. The specific epithet *ruginosa* is Latin for wrinkled and refers to the extensive ventral rugosities in these beetles. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "Entomology Division D.S.I.R. New Zealand"//"NEW CALEDONIA, Mt Do, 900 m, NW of Bouloupari, 22 Oct 1978, G.Kuschel"//"sifted litter and rotten wood, 78/249"//"EMEC201.498". NZAC. PARATYPE. Mt Do summit, 20 May 1984, G.Monteith & D.Cook, QM BERLESATE No. 654, 21.45S 166.00E, Rainforest, 1000 m, litter, EMEC1012127, ♀, QM.

Type locality. New Caledonia, Southern Province, Mt. Do. Estimated coordinates: 21° 45'S 165° 60'E.

Diagnosis. Among small sized-species with ventrally setose tarsomere 5 (e.g., *C. (B.) nana* and *C. (B.) orbiculata*), *C. (B.) ruginosa* is distinguished by the series of deep sulci above and behind the eye that are both numerous, and with at least two extended to the postocipital suture.

Description. *Size.* SBL 5.0 mm, greatest width over elytra 1.9 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with numerous well marked sulci. Eyes small, prominently convex. Ocular ratio 1.30. Antennae: overall

length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Paramedial pits deep, well defined, moderate size, diameter slightly less than 1/2 width between pits, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 112): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions present as a broad, deep, poorly defined depression that is continuous with broad flat area and reflex at hind angles, outer basal impressions absent, shape of lateral margins convergent in basal half, lateral marginal bead well defined from apical angle to slightly beyond hind angle and onto base, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture, 9 with 15 or 16 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells slightly transversely elongate, or somewhat irregular, forming mesh, luster moderately glossy. Elytral striae impressed moderately. Prosternum slightly, irregularly rugulose. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male slightly arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1 with lateral sulcus only, 2–5 without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI glabrous. Male genitalia (Fig. 131): orientation of median lobe of aedeagus in repose right side up. Orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broad, widening to apex, apex of median lobe in lateral view thick and reflexed ventrally, apex of median lobe in dorsal view broad, with medial apex produced as rounded lobe. Female genitalia and reproductive tract (Fig. 140): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 elongate, falcate, narrowly rounded apex, bursa short, left directed, common oviduct inserted near apex, right lateral portion of bursa with very large pouch, narrow at base, dorsal development of bursa lacking, spermatheca very short sessile, on common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at posterior oriented apex, gland duct length moderately elongate, gland duct with notable expanded region near base of gland, gland form spherical, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) sternovillosa sp. nov.
(Figs 99, 121, 146)

Etymology. The specific epithet *sternovillosa* is a compound word formed from the Latin *sterna-* for the abdominal ventrites and *-villosa*, hairy, and this draws attention to the pubescent last ventrite in these beetles. It is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "21°37′14″S/ 165°52′16″E NEW CALEDONIA, Prov.Sud. trail to Plateau de Dogny, 725 m 15:iii:2007, coll. KWill headlamp search, leaf litter"//" EMEC61788". Source EMEC, deposited MNHN. PARATYPES. Same data as holotype with EMEC61791, EMEC61794 and EMEC61790, 3♂♂, EMEC; EMEC61793, ♀, EMEC; EMEC61789, ♀, QM; EMEC61792 NC14 kww441, ♂, QM.

Type locality. New Caledonia, Southern Province, trail to Plateau de Dogny, 21° 37'S 165° 52'E.

Other material examined. Two additional males and one female, all very teneral, from the same locality as the holotype were examined, but are not included in the type series.

Diagnosis. Medium sized beetles with only two or three supra- and postorbital sulci, of which, only one reaches the post postocipital suture. This in combination with the presence of setae on the abdominal ventrites distinguish this species from others in the subgenus.

Description. *Size.* SBL 5.7–6.0 mm, greatest width over elytra 2.2–2.3 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with two to several well marked sulci. Eyes small, prominently convex. Ocular ratio 1.21–1.27. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, very small and blunt. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 99): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions present, short, shallow, broad, not well delimited, outer basal impressions absent, shape of lateral margins smoothly, moderately arcuate, broader across base than apex, lateral marginal bead well defined from apical angle to hind angle, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture, rarely with two setigerous punctures, 9 with 15 setigerous punctures. Elytra: color brunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster moderately glossy. Elytral striae impressed moderately. Prosternum rugosissimus across entire apical half. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture rugulose in anterior third. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres 1 with lateral sulcus only, 2–5 without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally with fine, short, scattered setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites:

ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI, apical margin in female entire, ventrites IV–VI with short scattered pubescence. Male genitalia (Fig. 121): orientation of median lobe of aedeagus in repose right side up, orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broad, widening to apex, apex of median lobe in lateral view thick and reflexed ventrally, apex of median lobe in dorsal view broad and emarginate. Female genitalia and reproductive tract: apical margin of gonocoxite-1 with two setae or with three setae, lateral edge of gonocoxite-2 with two ensiform setae, apical furrow of gonocoxite-2 with two nematiform setae, gonocoxite-2 moderately long, slightly curved, broadly rounded apex, bursa right side significantly longer than left, overall relatively stout, cup-shaped, right lateral portion of bursa with very large pouch, narrow at base, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) vitalis sp. nov.
(Figs 7, 93, 117, 138, 144)

Etymology. The specific epithet *vitalis* is from the Latin for "of life" and is treated as an adjective in the nominative singular.

Type material. HOLOTYPE, ♂. "21°37'14"S/165°52'16"E NEW CALEDONIA,Prov.Sud. trail to Plateau de Dogny 725–900 m, 15:iii:2007, coll. KWill headlamp search, leaf litter"//"EMEC61801". Source EMEC, deposited MNHN. PARATYPES. Same data as holotype with EMEC61795, EMEC61797, EMEC61798, EMEC61800, 4♂♂, EMEC and EMEC61796, EMEC61803, EMEC61804 NC15 kww42, EMEC61805, 4♀♀, EMEC. Same with EMEC61799, ♂, QM and EMEC61802, ♀, QM.

Type locality. New Caledonia, Southern Province, Plateau de Dogny, 21° 37'S 165° 52'E.

Diagnosis. *Cerabilia Biliacera vitalis* specimens with glabrous sternites are very similar to *C. (B.) klingonorum* (Figs 7–8) but are consistently smaller with sharper and better defined basal impressions on the pronotum (Fig. 93). Male genitalia (Fig. 117) is decisively different between these two species. *Cerabilia (B.) vitalis* with pubescent sternites are readily separated on that character state, and while similar in size and form to *C. (B.) klingonorum*, are likewise differentiated based on the pronotal impressions and male genitalia.

Description. *Size.* SBL 4.4–4.8 mm, greatest width over elytra 1.7–1.8 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with numerous well marked sulci. Eyes small, prominently convex. Ocular ratio 1.20–1.25. Antennae: overall length moderately long, with antennomere 11 just reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. Maxilla: antepenultimate palpomere plurisetose, with scattered short setae, penultimate palpomere plurisetose, with scattered short setae, apical palpomere plurisetose with short, scattered setae, palpomeres 2–4 apical distinctly longer than penultimate. *Thorax.* Pronotum (Fig. 93): microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions present, short, shallow, clearly marked, outer basal impressions absent, shape of lateral margins convergent in basal half, lateral marginal bead well defined from apical angle to hind angle, basal margin straight, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely angled, rounded not sharp, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals

slightly convex in apical third, flat in basal third, interval 3 with one setigerous puncture, 9 with 15 setigerous punctures. Elytra: color rufopiceous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells slightly transversely elongate, or somewhat irregular, forming mesh, luster moderately glossy. Elytral striae impressed moderately. Prosternum rugosissimus across entire apical half. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture rugulose in anterior third. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally glabrous, rarely ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. Female protarsomeres 1–4 dorsally glabrous, form not expanded, nearly symmetrical, ventrally with two rows of long setae on margins. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI of female with two pairs setae, ventrite VI apical margin in male entire, ventrite VI apical margin in female entire, ventrites IV–VI glabrous or VI with short scattered pubescence. *Male* genitalia (Fig. 117): orientation of median lobe of aedeagus in repose right side up, orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view arcuate and curved ventrally, blade of median lobe in ventral view broadly tapering, apex of median lobe in lateral view simple taper, apex of median lobe in dorsal view broadly rounded. Female genitalia and reproductive tract (Fig. 138): apical margin of gonocoxite-1 with two setae, lateral edge of gonocoxite-2 with two ensiform setae, gonocoxite-2 short, falcate, narrowly rounded apex, bursa right side significantly longer than left, overall relatively stout, cup-shaped, right lateral portion of bursa with very large pouch, narrow at base, dorsal development of bursa lacking, spermatheca very short sessile, at base of common oviduct, spermatheca duct not apparent, spermatheca broadly attached, spermathecal gland duct connected at base of spermatheca, gland duct length short, gland duct with notable expanded region near base of gland, gland form elongate ovoid, dorsal portion of bursa without modifications, ventral modification of bursa absent.

Cerabilia (B.) wisei sp. nov.

(Figs 103, 124, 146)

Etymology. The specific epithet *wisei* is treated as a noun in the genitive case and is in honor of Dr. D.M. Wise, MD for his contribution to research on *Cerabilia* by way of his treatment of me when I was injured due to an incident in the field.

Type material. HOLOTYPE, ♂. "NEW CALEDONIA, Prov. Sud., E of Table Unio, RP5, 390 m, (rd from Sarraméa to Canala) 17.iii.2007, R. Leschen"// "leaf litter, NC053, 21°33'49"S 165°45'37"E"// /"kww735"//"EMEC1000447". Source NZAC, deposited MNHN.

Type locality. New Caledonia, Southern Province, east of Table Unio 21°33'S 165°45'E.

Diagnosis. Similar in size and form to *C. (B.) vitalis*. See diagnosis under that species.

Description. *Size.* SBL 4.1 mm, greatest width over elytra 1.6 mm. *Head.* Dorsal microsculpture with sculpticells isodiametric or somewhat irregular in form, microlines forming mesh. Supra- and postorbital region with numerous well marked sulci. Eyes small, prominently convex. Ocular ratio 1.20. Antennae: overall length long, with antennomeres 10–11 reaching beyond pronotal base, antennomere 3 not pubescent, with ring of fine small setae at apex. Labral apical margin with six setae. Labial penultimate palpomere with two large medial setae and 1–2 small apical setae. Glossal sclerite form broadly rounded at apex, edge thin, sloping ventrally. Mentum anterior margin moderately emarginate, tooth simple, blunt, triangular. Paramedial pits deep, well defined, large, diameter equal to 1/2 width between pits or larger, paramedial pits glabrous. *Thorax.* Pronotum (Fig. 103):

microsculpture sculpticells isodiametric or somewhat irregular in form, microlines forming mesh, macrosculpture smooth, inner basal impressions present, shallow, but defined medially, not delimited laterally, blending into broad depression, outer basal impressions absent, shape of lateral margins smoothly, shallowly arcuate, lateral marginal bead well defined from apical angle to hind angle, basal margin very shallowly emarginate in middle, anterior margin medially broadly emarginate, apical angles prominent, hind angles obtusely rounded, anteriolateral setae very near margin, touching channel of lateral margin or approximately width of setal pore distant from lateral margin. Elytron with nine intervals, form of intervals flat, slightly more convex near apex, interval 3 with one setigerous puncture, 9 with 15 setigerous punctures. Elytra: color brunneous, macrosculpture many very small punctulae just visible at 50x, microsculpture sculpticells transversely elongate, longitudinally short relative to body axis, luster moderately glossy. Elytral striae impressed moderately. Prosternum rugosissimus across entire apical half. Proepisternum rugosissimus. Metepisternum macrosculpture rugosissimus. Metepimerion macrosculpture smooth, or with rugosities just at anterior edge. Mesosternum macrosculpture rugosissimus. Tarsomere 5 on all legs ventrally setose (at least one pair of long setae, usually with several smaller setae). Mesofemur posterior face macrosculpture smooth. Mesotarsomeres without sulci. Metatibia of male arcuate. Metafemur of male with ventral margin straight or smoothly, shallowly arcuate. Metatarsomeres without sulci. Dorsal surface of meso- and metatarsomeres glabrous. Male protarsomeres 1–3 dorsally glabrous or with a few very small setae, form broadly expanded, asymmetrical, ventrally with two rows large articulo-seta, 4 with elongate apical setae. *Abdomen.* Sternites: ventrite VI of male with one pair of setae, ventrite VI apical margin in male entire, ventrites IV–VI with short scattered pubescence. Male genitalia (Fig. 124): orientation of median lobe of aedeagus in repose right side up, orientation of ostium dorsal, form of right paramere conchoid, larger, left smaller and blunt, median lobe in lateral view right angled, blade of median lobe in ventral view broad, widening to apex, apex of median lobe in lateral view thick and reflexed ventrally, apex of median lobe in dorsal view blunt. Female genitalia and reproductive tract: female unknown.

Key to adults of *Cerabilia* in the subgenera *Feronista* and *Biliacera*.

The species treatments above are listed alphabetically within each subgenus as per the journal requirements. The page number for each species description is therefore included in the Key. The figures of morphological features are, for the most part, arranged in the order that the species emerge from the key to facilitate comparison of similar species.

1. Pronotum with posterolateral seta. Third elytral interval without setigerous punctures. Australia. Subgenus *Feronista*. 2
– Pronotum without posterolateral seta. Third elytral interval with 1-5 setigerous punctures. New Caledonia. Subgenus *Biliacera*.. 31

2. Elytron with nine intervals. 3
– Elytron with rudimentary tenth interval in apical third or more. Tenth interval entire or irregularly interrupted where evident. 15

3. Mesotarsomere 1 with evident lateral and medial sulci (medial sulci short and shallow in some specimens of *C. (F.) minor* and *C. (F.) montivaga*). 4
– Mesotarsomere 1 without sulci or with lateral sulcus only (some specimens of *C. (F.) lewisensis* and *C. (F.) spinifer* with dorsal sulci that are short and shallowly impressed 26

4. Antennomere 3 pubescent in apical third to half. 5
– Antennomere 3 glabrous except for apical ring of long, fine setae. 6

5. Pronotum posteromedial impressions shallow, linear or nearly punctiform (Fig. 10) . . . . . *Cerabilia (F.) securilata,* pg. 45

– Pronotum posteromedial impression absent (Fig. 11). . *Cerabilia (F.) spuh,* pg. 47

6. Metatarsomere 1 with lateral and medial sulci (sulci very shallow in *C. (F.) minor*) . . .7

– Metatarsomere 1 with lateral sulcus only, medial sulcus absent. 11

7. Elytra with 13-14 umbilicate marginal pores. Meso- and metatarsomere 4 without medial and lateral sulci 8

– Elytra with 15-16 umbilicate marginal pores. Meso- and metatarsomere 4 with medial and lateral sulci 10

8. Hind angles of pronotum broadly and obtusely angled, nearly rounded (Figs 13-14) 9

– Hind angles of pronotum narrowly, obtusely angled, approaching right angled (Fig. 12). . . . . *Cerabilia (F.) minor,* pg. 34

9. Abdominal sterna with a glossy luster, microsculpture stretched and scarcely evident. . . . . *Cerabilia (F.) montivaga,* pg. 36

– Abdominal sterna dull along lateral third, moderately glossy medially, microsculpture conspicuous, forming a stretched and irregular mesh. . *Cerabilia (F.) blatta,* pg. 24

10. Pronotal hind angles moderately obtusely angled, slightly reflexed and flat anterad hind seta (Fig. 15) . . . . . *Cerabilia (F.) australiensis,* pg. 19

– Pronotal hind angles broadly rounded, not reflexed and slightly convex anterad hind seta (Fig. 16). . *Cerabilia (F.) iridescens,* pg. 30

11. Mesepisternum smooth or very slightly rugulose. Pronotum posteromedial impressions not evident 12

– Mesepisternum with shallow punctulae and slightly rugulose. Pronotum posteromedial impressions slightly or clearly evident (Fig. 17). . . . . *Cerabilia (F.) storeyi,* pg. 48

12. Pronotal margins moderately to deeply arcuate. Antennomeres 8-10 long, length about 2.5-3.0x width. SBL>5.0mm 13

– Pronotal margins very shallowly arcuate (Fig. 18) Antennomeres 8-10 short, length not more than 2.0x width. SBL<4.0 mm . . . . . *Cerabilia (F.) parva,* pg. 41

13. Anteroventral aspect of the mesepisternum with a distinct bulge set off from the elytral epipleura and the medial portion of the mesepisternum. Proepisternum glossy with scarcely visible, irregular or slightly stretched microsculpture 14

– Anteroventral aspect of the mesepisternum without a distinct bulge. Proepisternum somewhat dull, with visible, stretched microsculpture . . . . . *Cerabilia (F.) danbullaensis,* pg. 25

14. Elytra marginal umbilicate pores 1-3 in contact with lateral channel. SBL>6.5 mm . . . . . *Cerabilia (F.) kalkajaka,* pg. 31

– Elytra marginal umbilicate pores 1-6 in contact with lateral channel. SBL<6.0mm . . . . . *Cerabilia (F.) uncata,* pg. 52

15. Microsculpture of metepisternum clearly visible irregular mesh, isodiametric, or not apparent and with only slight iridescence 16

– Microsculpture of metepisternum stretched, somewhat irregular mesh with a more or less clear iridescence or not visible at 50x magnification 18

16. Metatarsomere 4 with medial and lateral sulci. SBL>6.0 mm. 17

– Metatarsomere 4 without sulci. SBL<5.5mm . . . . . *Cerabilia (F.) reflexa,* pg. 44

17. Metatibia with medial row of nine (range 8-10) fine setae. SBL>8.0mm . . . . . *Cerabilia (F.) loxandroides* pg. 33

– Metatibia with medial row of four (range 3-6) fine setae. SBL<7.5 mm . . . . . *Cerabilia (F.) moorei,* pg. 37

18. Elytral intervals with dense, obvious micropunctulae 19

– Elytral intervals without micropunctulae or with only a few scattered punctulae 21

19. Pronotum microsculpture obvious irregular mesh 20

– Pronotum microsculpture scarcely visible at 50x magnification, stretched . . . . . *Cerabilia (F.) gigas,* pg. 26

20. Posteromedial and posterolateral pronotal

impressions apparent as very broad shallow depressions. Pronotal base slightly convex laterad posterolateral impression (Fig. 28) ..... *Cerabilia (F.) tipica,* pg. 51

– Posterior pronotal impressions not apparent. Pronotal base depressed, flat laterad posterolateral impression (Fig. 25) ..... *Cerabilia (F.) haigensis,* pg. 28

21. Pronotal hind angles broadly rounded obtuse..... 22

– Pronotal hind angles narrowly obtuse, nearly right angled..... 24

22. Stria 7 with two setigerous punctures near the apex. SBL<8.8 mm. 23

– Stria 7 with three setigerous punctures near the apex. SBL>9.4 mm ..... *Cerabilia (F.) amaroides,* pg. 21

23. Elytral microsculpture transverse and obvious ..... *Cerabilia (F.) stylata*

– Elytral microsculpture not visible at 50x magnification . . *Cerabilia (F.) mudda,* pg. 39

24. Pronotum (Figs 32-33) with the anterior marginal seta about 1.5-2x the pore width from the margin. Base of pronotum without demarcated margin. 25

– Pronotum (Fig. 31) with the anterior marginal setigerous pore touching or very near the marginal channel. Lateral marginal bead continuous on base of pronotum, demarcating margin for about one the basal width ..... *Cerabilia (F.) intermedia,* pg. 29

25. Male with metatrochanter with deep dorsal concavity (Fig. 147) ..... *Cerabilia (F.) prosopogmoides,* pg. 43

– Male with metatrochanter dorsally flat as typical in genus . *Cerabilia (F.) prolixa,* pg. 42

26. Humeri of elytra rounded angulate, without denticle. Overall form slightly elongate ovoid. SBL<5.7 mm. 27

– Humeri of elytra with small, sharp denticle. Overall form distinctly ovoid SBL>5.8 mm ..... *Cerabilia (F.) oodiformis,* pg. 40

27. Elytral striae impunctate..... 28

– Elytral striae crenulate or minutely punctate 30

28. Elytra uniformly brunneous, piceous or only vaguely paler along interval 1, the apex, and lateral margins. 29

– Elytra broadly and distinctly paler on interval 1, the lateral margins, and apically ..... *Cerabilia (F.) lewisensis,* pg. 32

29. Pronotum lateral margins smoothly arcuate from apex to base (Fig. 36). Anterior seta very near or touching the lateral channel. Prosternal process rounded ..... *Cerabilia (F.) wunduensis,* pg. 53

– Pronotum lateral margins slightly convergent to base from just anterad mid-point (Fig. 37). Anterior seta a pore width or more from the lateral channel. Prosternal process bluntly truncate ..... *Cerabilia (F.) spinifer,* pg. 46

– Pronotal basal seta in lateral bead. Lateral marginal bead continuous on base of pronotum, demarcating margin for about one third the basal width ..... *Cerabilia (F.) monteithi,* pg. 35

– Pronotal basal seta not in lateral bead. Lateral marginal bead ended anterad basal seta. ..... *Cerabilia (F.) bellensis,* pg. 23

30. Supra- and postorbital region with two, to many, sulcate rugosities (Fig. 148)..... 32

– Supra- and postorbital region smooth. . 37

31. Prosternum rugosissumus across entire anterior third or more. 33

– Prosternum only lightly, irregularly rugulose or smooth in the anteromedial third, when rugosities present restricted, to anterior margin in anterior third or less, laterally rugosissumus, rugulose or smooth..... 42

32. Supra- and postorbital rugosities consisting of 3 or more sulci, two or more sulci in contact with the postocipital suture 34

– Supra- and postorbital rugosities consisting of 2 or 3, often very short sulci, only one sulcus in contact with the postocipital suture..... 44

33. Ventrite VI glabrous..... 35

– Ventrite VI with short scattered pubescence 47

34. Mentum tooth prominent, form simple triangle. Metepimeron rugose 36
— Mentum tooth not prominent, short and wide, almost absent. Metepimeron smooth except near anterior edge . . . . . *Cerabilia (B.) apicesecta,* pg. 56

35. Pronotum (Fig. 92) dorsally, in anterior third, with scattered very fine punctulae; basal impressions very shallowly impressed, linear or irregularly formed. SBL >4.8 mm . . . . . *Cerabilia (B.) klingonorum,* pg. 66
— Pronotum (Fig. 93) dorsally smooth or with some very fine punctulae; basal impressions sharply impressed, linear. SBL <4.8 mm . . . . . *Cerabilia (B.) vitalis,* pg. 79 (in part)

36. Pronotal anteriolateral seta near, about one pore width distant at most, or touching lateral channel or bead. 38
— Pronotal anteriolateral seta very distant from lateral channel or bead, three pore widths or greater distance (Figs 104-107) 48

37. Mesotarsomere 1 without sulci 39
— Mesotarsomere 1 with lateral and medial sulci 51

38. Elytral interval 3 with one setigerous puncture 40
— Elytral interval 3 with two or three setigerous punctures 52

39. Pronotal basal impressions parallel with the longitudinal axis of the body 41
— Pronotal basal impression slightly divergent, parallel with the convergent lateral margins in the basal third of the pronotum . . . *Cerabilia (B.) mouensis* pg. 70

40. Region laterad of pronotal basal impression a low convexity . . . . . *Cerabilia (B.) kanakorum*pg. 65
— Region laterad of pronotal basal impression flat and depressed to the margin . . . . . *Cerabilia (B.) rubrica* pg. 75

41. Tarsomere 5 ventrally glabrous. 43
— Tarsomere 5 ventrally setose 53

42. Paramedial pits of mentum large, diameter equal to ½ the width of the space between the pits or more . . *Cerabilia (B.) letalis,* pg. 69
— Paramedial pits of mentum small, diameter much less than ½ the width of the space between the pits . *Cerabilia (B.) drupa,* pg. 59

43. Ventrites IV-VI glabrous except for fixed paramedial pair of setae 45
— Ventrites IV-VI with short scattered pubescence . *Cerabilia (B.) sternovillosa,* pg. 78

44. Antennomere 3 glabrous except for an apical ring of fine setae 46
— Antennomere 3 pubescent in the apical third to half. . . . . *Cerabilia (B.) paniensis,* pg. 74

45. Male profemur relatively slender, metatibia slightly, smoothly curved, aedeagus narrowing apicad. Female unknown . . . . . *Cerabilia (B.) amieuensis,* pg. 55
— Male profemur robust, with an inflated appearance, metatibia with angulate bend, aedeagus wide at apex . . . . . *Cerabilia (B.) inversa,* pg. 64

46. Pronotal basal impressions sharply delimited, linear, and clearly impressed (Fig. 93) . . . . . *Cerabilia (B.) vitalis,* pg. 79 (in part)
— Pronotal basal impressions broad and not delimited laterally (Fig. 103) . . . . . *Cerabilia (B.) wisei,* pg. 80

47. Elytral interval 3 with one (rarely, unilaterally two) setigerous puncture . . 49
— Elytral interval 3 with four to five setigerous punctures . *Cerabilia (B.) discosetosa,* pg. 57

48. Mentum tooth absent . . . . . *Cerabilia (B.) edentata,* pg. 60
— Mentum tooth present 50

49. Pronotum widest at midpoint of its length, basal margin with a deep rounded emargination . *Cerabilia (B.) koghisensis,* pg. 68
— Pronotum widest behind midpoint of its length, basal margin straight . . . . . *Cerabilia (B.) aite,* pg. 54

50. Elytral interval 3 with one setigerous puncture . . . . . *Cerabilia (B.) espee,* pg. 62
— Elytral interval 3 with three setigerous punctures . . *Cerabilia (B.) neocaledonica,* pg. 72

51. Mesosternum and metepisternum rugosissimus . . *Cerabilia (B.) francisca* pg. 63

— Mesosternum and metepisternum smooth or scabriculous . . *Cerabilia (B.) dominatrix,* pg. 58

52. Supraorbital region with two sulci, only one sulcus in contact with the postocipital suture. Eyes moderately convex. 54

— Supraorbital region with numerous sulci, two or more sulci in contact with the postocipital suture. Eyes small and prominent . . . . . *Cerabilia (B.) ruginosa,* pg. 76

53. Form of elytra slightly elongate ovoid, SBL=3.4 mm . . . . *Cerabilia (B.) nana,* pg. 71

— Form of elytra rounded ovoid, SBL=4.0 mm . . . . . *Cerabilia (B.) orbiculata,* pg. 73

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LITERATURE CITED

Alvarez-Padilla, F.A. & Hormiga, G. 2007, 2008. A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. *The Journal of Arachnology.* **35**: 538–542 https://doi.org/10.1636/Sh06-55.1.

Baehr, M. 2007. A new genus of cyclosomine carabid beetles from Queensland, Australia. *Mitteilungen der Münchner Entomologischen Gesellschaft.* **97**: 5–9.

Bonelli, F.A. (1810) Observations entomologiques. Première partie (cicindélètes et portion des carabiques) [with the "Tabula synoptica exhibens genera carabicorum in sectiones et stirpes disposita"]. Turin. 58 pp. + 1 table. Note. The paper was reissued in 1812, without the "Tabula Synoptica," in *Memorie della Reale Accademia della Scienze di Torino* 18: 21-78 (see Madge 1978, Bull. Zool. *Nomencl.* 35: 9-12).

Bowie, M. 2008a. Ecological restoration of the invertebrate fauna on Quail Island (Ō tamahua). *Conserv-Vision Conference Proceedings The University of Waikato,* 2–4.

Bowie, M. 2008b. Bio-Protection & Ecology Division Measuring the diversity and abundance of carabids. *Lincoln University Wildlife Management Report* No. 44.

Broun, T. 1893. *Manual of the New Zealand Coleoptera. Parts V–VII: XVII + 975–1504.* New Zealand Institute, Wellington.

Broun, T. 1910. Descriptions of new genera and species of Coleoptera. *Bulletin of the New Zealand Institute* **1**: 1–78.

Broun, T. 1912. Descriptions of new genera and species of Coleoptera. [Part I]. *Transactions and Proceedings of the New Zealand Institute* 44 (1911): 379–440.

Chaudoir, M d. 1873. Essai monographique sur les drimostomides et les cratocérides et description d'un genre nouveau de morionides. *Annales de la Société Entomologique de Belgique* **15**: 5-24.

Chaudoir, M d. 1878. Descriptions de genres nouveaux et d'espèces inédites de la famille des carabiques. *Bulletin de la Societe imperiale des naturalistes de Moscou,* **53**, 1–80.

Erwin, T.L. & Sims, L.L. 1984. Carabid beetles of the West Indies (Insects: Coleoptera): A synopsis of the genera and checklists of the tribes of Caraboidea, and of the West Indian species. *Quaestiones entomologicae* **20**: 351-466.

Guéorguiev, B. & Sciaky, R. 2015. A new genus and two new species of Pterostichini from China, with "sphodrine-like" parameres (Coleoptera, Carabidae). *Deutsche Entomologische Zeitschrift.* **62**(2): 225–237 https://doi.org/10.3897/dez.62.5493.

Laporte, F.L. 1867. Notes on Australian Coleoptera. *Transactions and Proceedings of the Royal Society of Victoria,* 139, 1–139.

Laporte, F.L. 1868. Notes on Australian Coleoptera. *Transactions and Proceedings of the Royal Society of Victoria,* 8, 30–38, 95–225.

Larochelle, A. & Larivière, M.-C. 2001. Carabidae (Insecta: Coleoptera): Catalogue. *Fauna of New Zealand,* Manaaki Whenua-Landcare Research New Zealand, Lincoln. **43**, pp. 285.

Larochelle, A. & Larivière, M.-C. 2005. *Harpalini* (Insecta: Coleoptera: Carabidae: Harpalinae). Fauna of New Zealand, *Manaaki Whenua-Landcare Research* New Zealand, Lincoln. **53**, pp. 160.

Larochelle, A. & Larivière, M.-C. 2007. Carabidae (Insecta: Coleoptera): synopsis of supraspecific taxa. *Fauna of New Zealand*, Manaaki Whenua-Landcare Research New Zealand, Lincoln. **60,** pp. 188.

Larochelle, A. & Larivière, M.-C. 2016. Taxonomic Supplement (2001 to 2015) to the Catalogue of New Zealand Carabidae (Insecta: Coleoptera). *Insecta Mundi*. **O502**: 1–53.

LeConte, J.L. 1853. Synopsis of the species of Pterostichus Bon. and allied genera inhabiting temperate North America. J*ournal of the Academy of Natural Sciences of Philadelphia* (series 2) **2** [1850-54]: 225-256

Liebherr, J.K. & Will, K.W. 1998. Inferring phylogenetic relationships within Carabidae (Insecta, Coleoptera) from characters of the female reproductive tract. Pp 107–170. *In*, Phylogeny and Classification of Caraboidea Coleoptera: Adephaga). *Proceedings of a Symposium* (28 August, 1996, Florence, Italy) (Eds G.E. Ball, A. Casale & A.V. Taglianti), pp. 107–170. XX International Congress of Entomology. *Atti Museo Regionale di Scienze Naturali di Torino*. Italy.

Liebherr, J.K. & Will, K.W. 2015. Antisymmetric male genitalia in Western Australian populations of *Mecyclothorax punctipennis* (Coleoptera: Carabidae: Moriomorphini). *Insect Systematics & Evolution*. **46**(4): 1–17. https://doi.org/10.1163/1876312X-45042124.

Lorenz, W. 2005a. *Nomina Carabidarum - A Directory of the Scientific Names of Ground Beetles (Coleoptera "Geadephaga": Trachypachidae and Carabidae, incl. Paussinae, Cicindelinae, Rhysodinae)*. Tutzing.

Lorenz, W. 2005b. *A Systematic List of Extant Ground Beetles of the World (Coleoptera "Geadephaga": Trachypachidae and Carabidae, incl. Paussinae, Cicindelinae, Rhysodinae)*. Tutzing.

Lorenz, W. 2018. *CarabCat-Checklist.* http://www.carabidfauna.com. Accessed 4 April 2019.

Monteith, G.B. (2018) Barry Philip Moore, 1925–2015, coleopterist, chemist and natural historian. *The Australian Entomologist.* **45**: 325.

Moore, B.P. 1965. Studies on Australian Carabidae (Coleoptera) 4.–The Pterostichinae. *Transactions of the Royal entomological Society of London*. **117**: 1–32 https://doi.org/10.1111/j.1365-2311.1965.tb00042.x.

Moore, B.P., Weir, T.A. & Pyke, J.E. 1987. Rhysodidae and Carabidae. *In,* Zoological Catalogue of Australia. In *vol. 4 (Coleoptera: Archostemata, Myxophaga and Adephaga)* (ed D.W. Walton), pp. 20–230. (Australian Government Publishing Service: Canberra, ACT).

Roddenberry, G. (1979) *Star Trek, the motion picture: a novel*. New York: Pocket Books, 256pp.

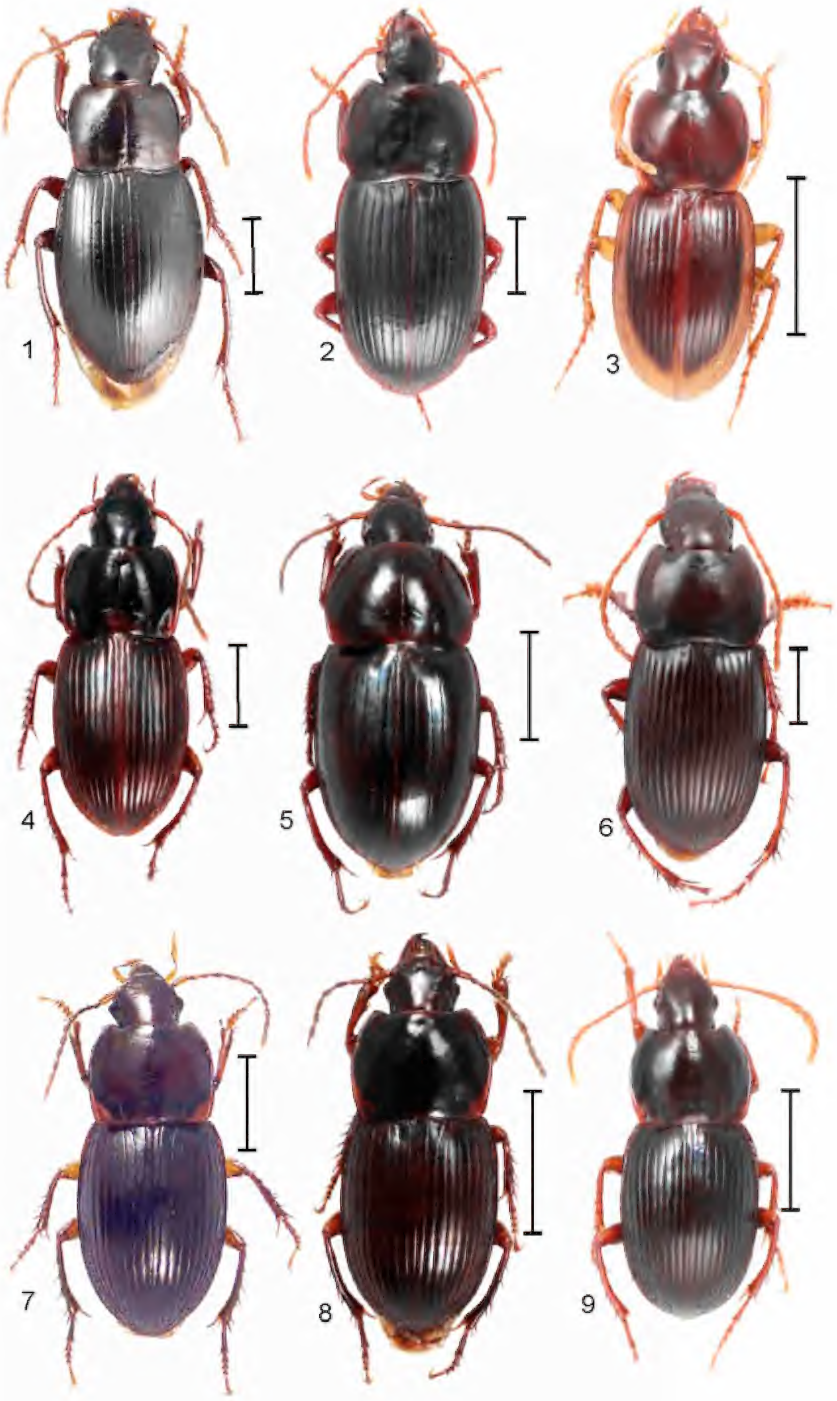
Straneo, S.L. 1991. South American species of Loxandrus LeConte, 1852 (Coleoptera: Carabidae: Pterostichini). *Annals of Carnegie Museum,* **60**: 1–62.

Torre-Bueno JRdl. 1989. The Torre-Bueno glossary of entomology. Revised edition. (New York, N.Y., USA: New York Entomological Society in cooperation with the American Museum of Natural History).

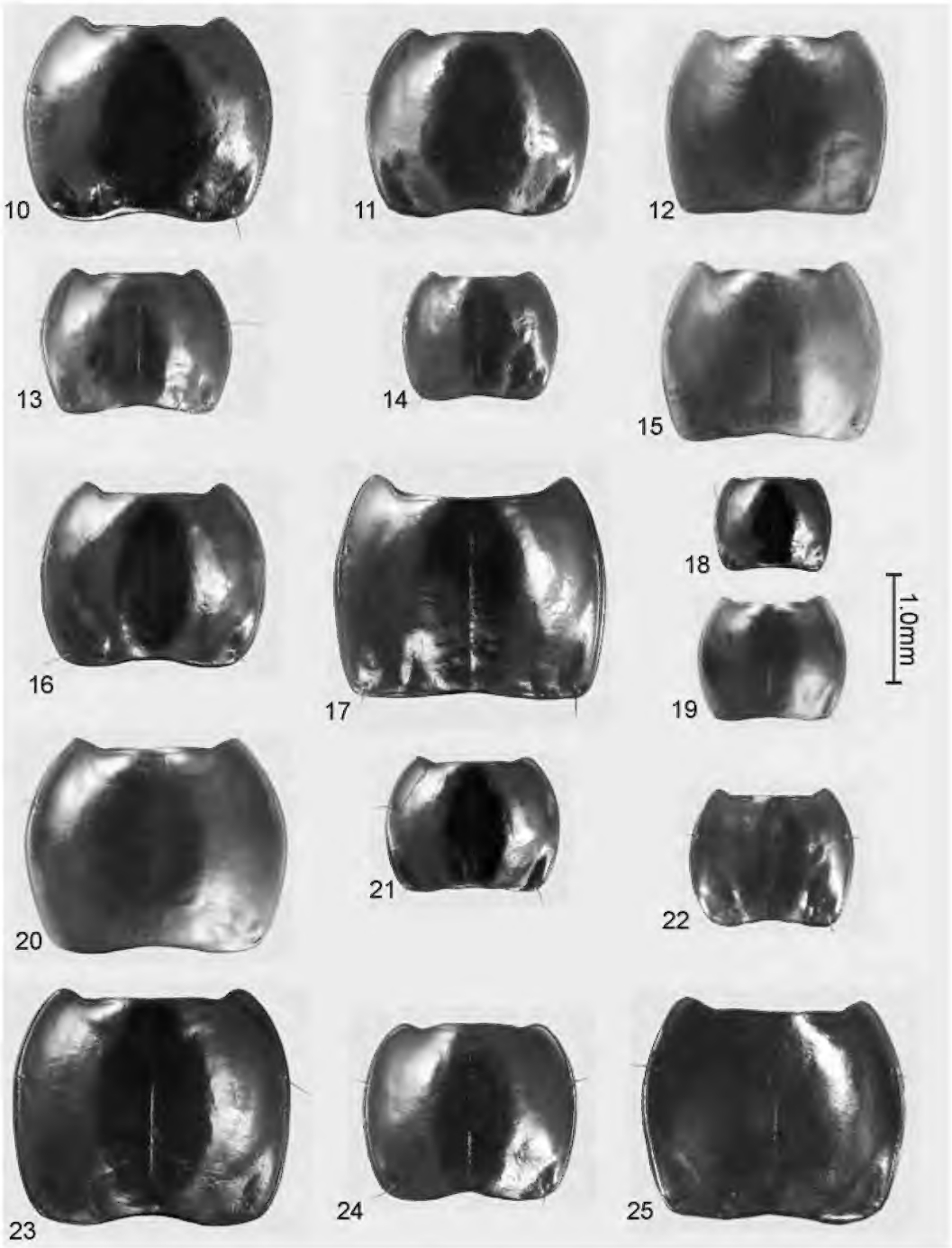
Watts, C., Thornburrow, D., Cave, V. & Innes, J. 2014. Beetle community changes following pest mammal control at two biodiversity sanctuaries in Wellington, New Zealand. *Journal of the Royal Society of New Zealand.* **44**: 61–87 https://doi.org/10.1080/03036758.2013.875478.

Will, K.W. 2011. Taxonomic review of the Pterostichini and Loxandrini fauna of New Caledonia (Coleoptera, Carabidae). *ZooKeys*. **147**: 337–397 https://doi.org/10.3897/zookeys.147.1943.

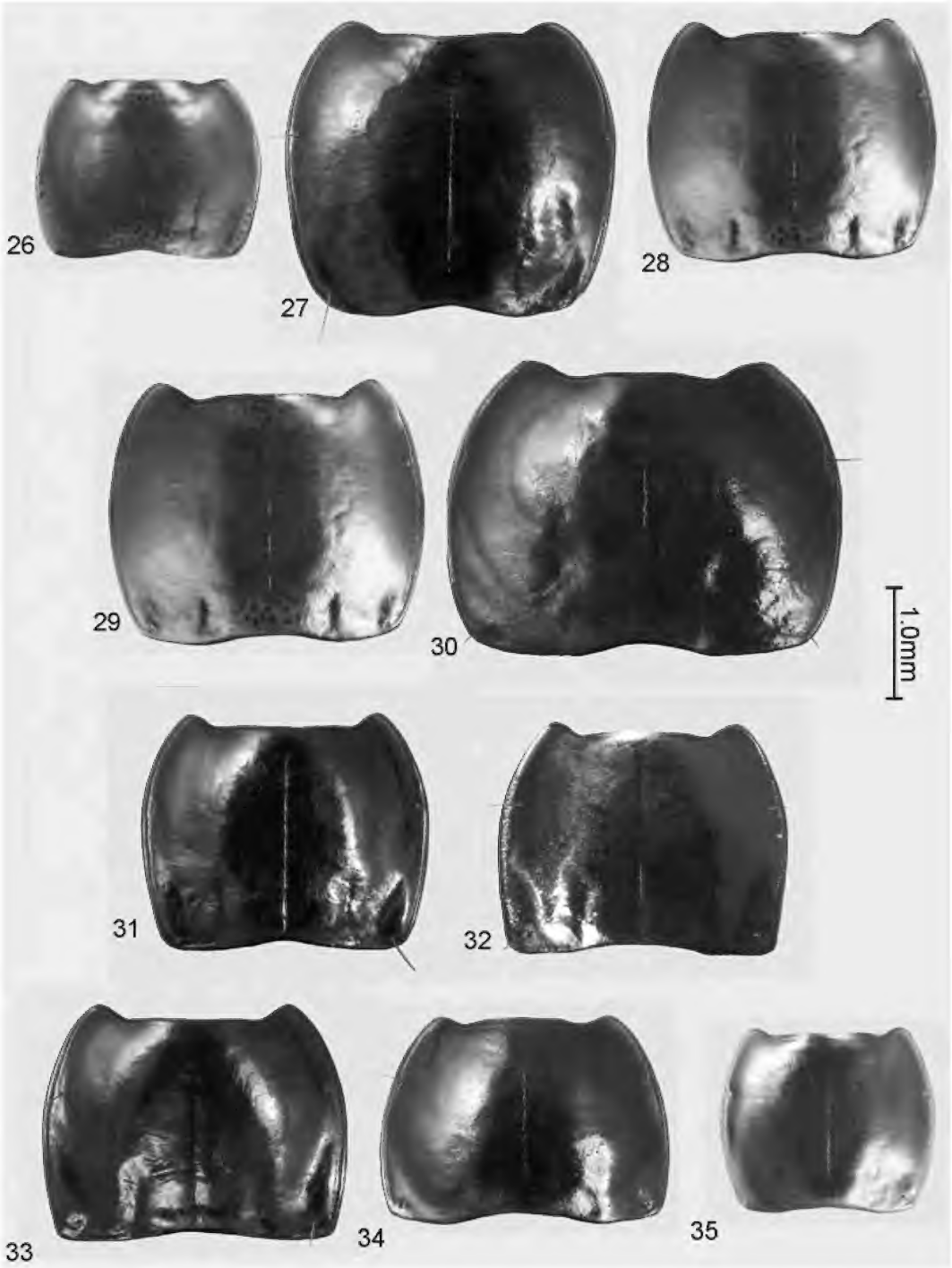
Will, K.W. 2015. Resolution of taxonomic problems in Australian Harpalini, Abacetini, Pterostichini, and Oodini (Coleoptera, Carabidae). *ZooKeys*. **545**: 131–137 https://doi.org/10.3897/zookeys.545.6752.



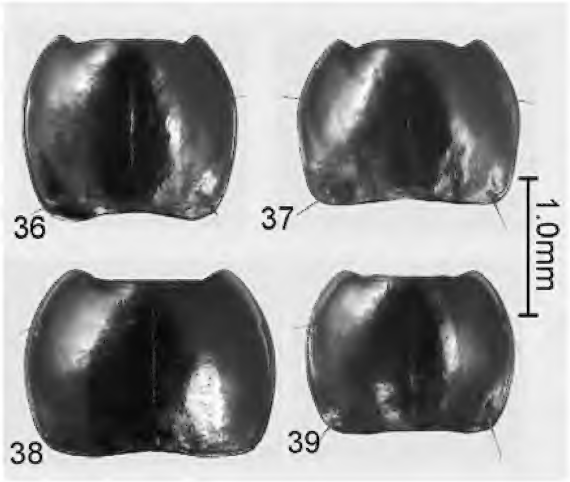
FIGS 1–9. Dorsal habitus of 1. *Cerabilia (Cerabilia) striatula;* 2. *C. (Feronista) amaroides;* 3. *C. (F.) lewisensis;* 4. *C. (F.) storeyi;* 5. *C. (F.) oodiformis;* 6. *C. (Biliacera) discosetosa;* 7. *C. (B.) vitalis;* 8. *C. (B.) klingonorum;* 9. *C. (B.) espee*. Scale bars= 2.0 mm.



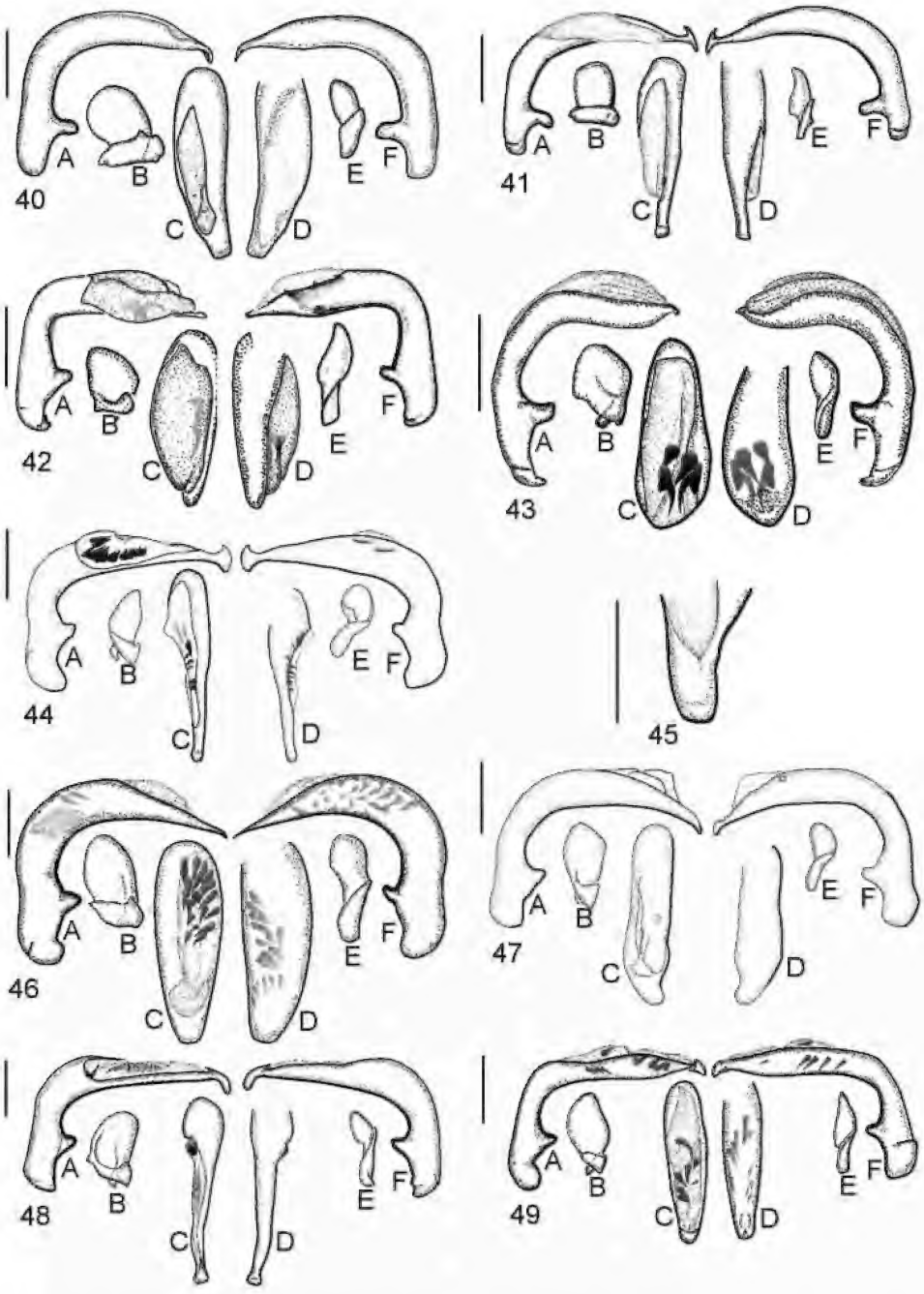
FIGS 10–25. Pronota of *Cerabilia (Feronista)* spp. 10. *C. (F). securilata*; 11. *C. (F). spuh*; 12. *C. (F). minor*; 13. *C. (F). montivaga*; 14. *C. (F). blatta*; 15. *C. (F). australiensis*; 16. *C. (F). iridescens*; 17. *C. (F). storeyi*; 18. *C. (F). parva*; 19. *C. (F). danbullaensis*; 20. *C. (F). kalkajaka*; 21. *C. (F). uncata*; 22. *C. (F). reflexa*; 23. *C. (F). loxandroides*; 24. *C. (F). moorei*; 25. *C. (F). haigensis*.



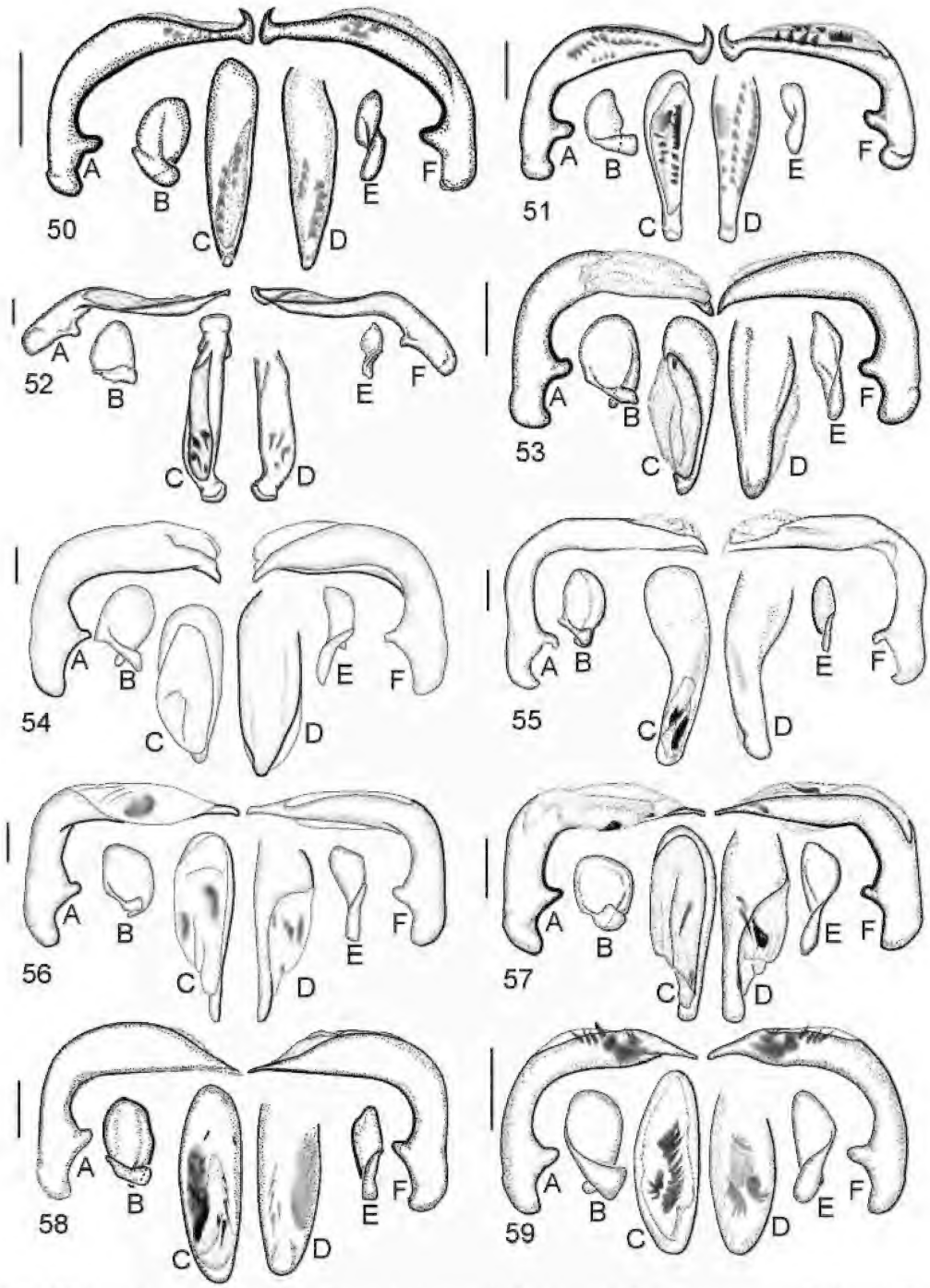
FIGS 26–35. Pronota of *Cerabilia (Feronista)* spp. 26. *C. (F). stylata*; 27. *C. (F). gigas*; 28. *C. (F). tipica*; 29. *C. (F). amaroides*; 30. *C. (F). mudda*; 31. *C. (F). intermedia*; 32. *C. (F). prosopogmoides*; 33. *C. (F). prolixa*; 34. *C. (F). oodiformis*; 35. *C. (F). lewisensis*.



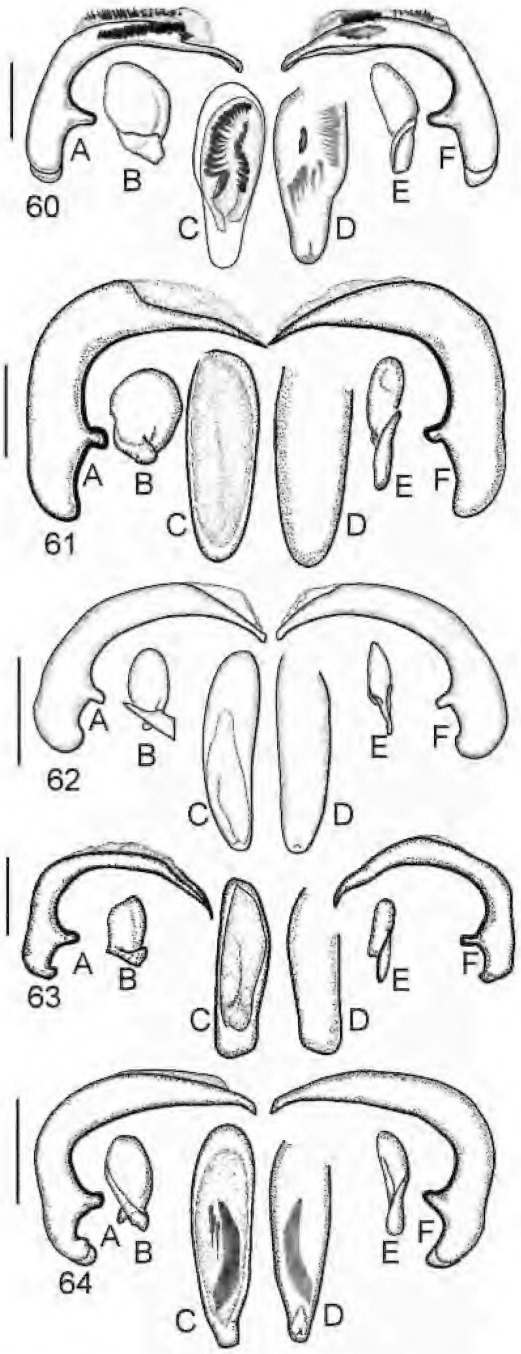
FIGS 36–39. Pronota of *Cerabilia (Feronista)* spp. 36. *C. (F). wunduensis*; 37. *C. (F). spinifer*; 38. *C. (F). monteithi*; 39. *C. (F). bellensis*.



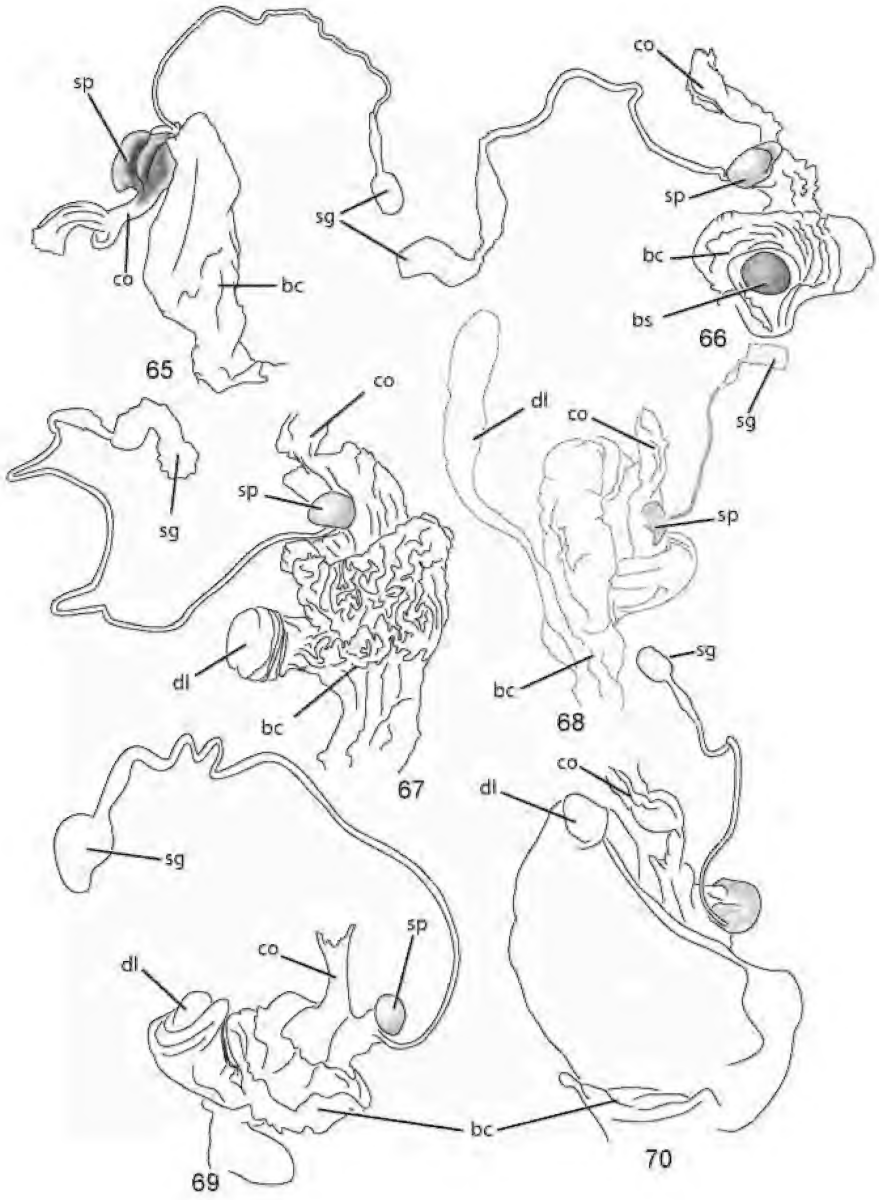
FIGS 40–49. Male aedeagus of *Cerabilia (Feronista)* spp., A- left lateral, B- left paramere, C-dorsal, D-ventral, E-right paramere, F-right lateral views. Scale bars are 0.5 mm. 40. *C. (F). securilata*; 41. *C. (F). spuh*; 42. *C. (F). minor*; 43. *C. (F). montivaga*; 44. *C. (F). blatta*; 45. *C. (F). iridescens*, Dorsal view, tip; 46. *C. (F). storeyi*; 47. *C. (F). danbullaensis*; 48. *C. (F). kalkajaka*; 49. *C. (F). uncata*.



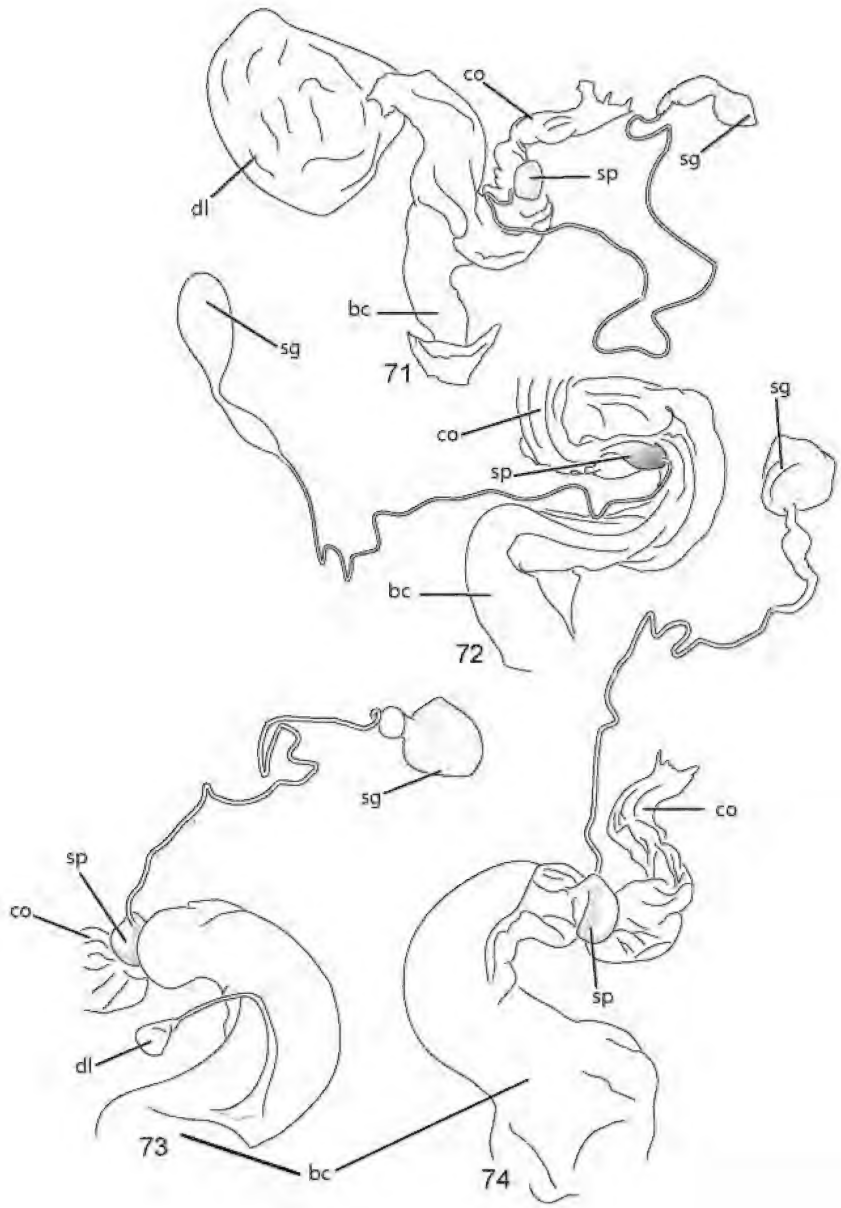
FIGS 50–59. Male aedeagus of *Cerabilia (Feronista)* spp., A- left lateral, B- left paramere, C-dorsal, D-ventral, E-right paramere, F-right lateral views. Scale bars are 0.5 mm. 50. *C. (F). reflexa*; 51. *C. (F). moorei*; 52. *C. (F). gigas*; 53. *C. (F). tipica*; 54. *C. (F). haigensis*; 55. *C. (F). amaroides*; 56. *C. (F). stylata*; 57. *C. (F). mudda*; 58. *C. (F). intermedia*; 59. *C. (F). prosopogmoides*.



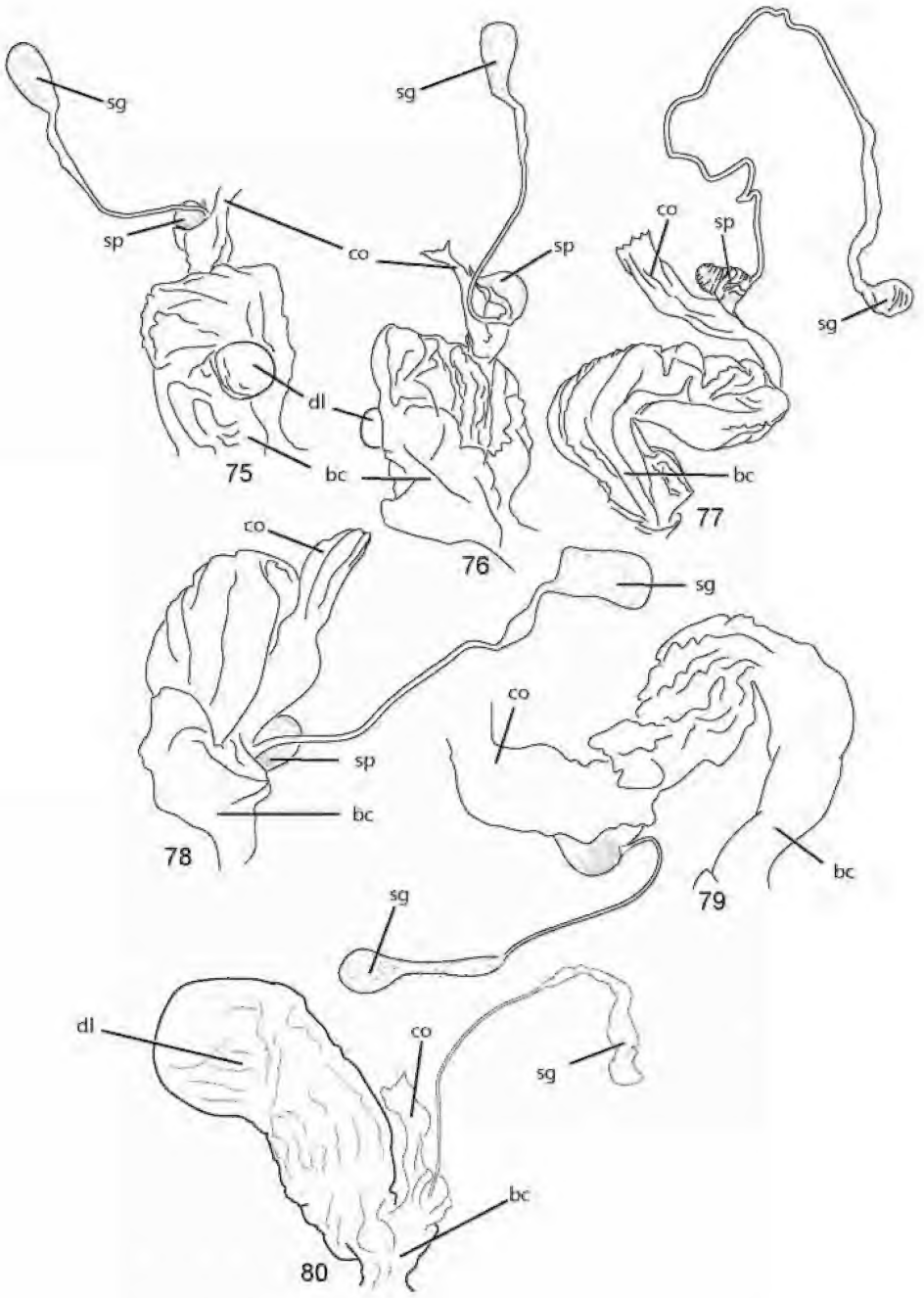
FIGS 60–64. Male aedeagus of *Cerabilia (Feronista)* spp., A- left lateral, B- left paramere, C-dorsal, D-ventral, E-right paramere, F-right lateral views. Scale bars are 0.5 mm. 60. *C. (F). prolixa*; 61. *C. (F). oodiformis*; 62. *C. (F). lewisensis*; 63. *C. (F). monteithi*; 64. *C. (F). bellensis*.



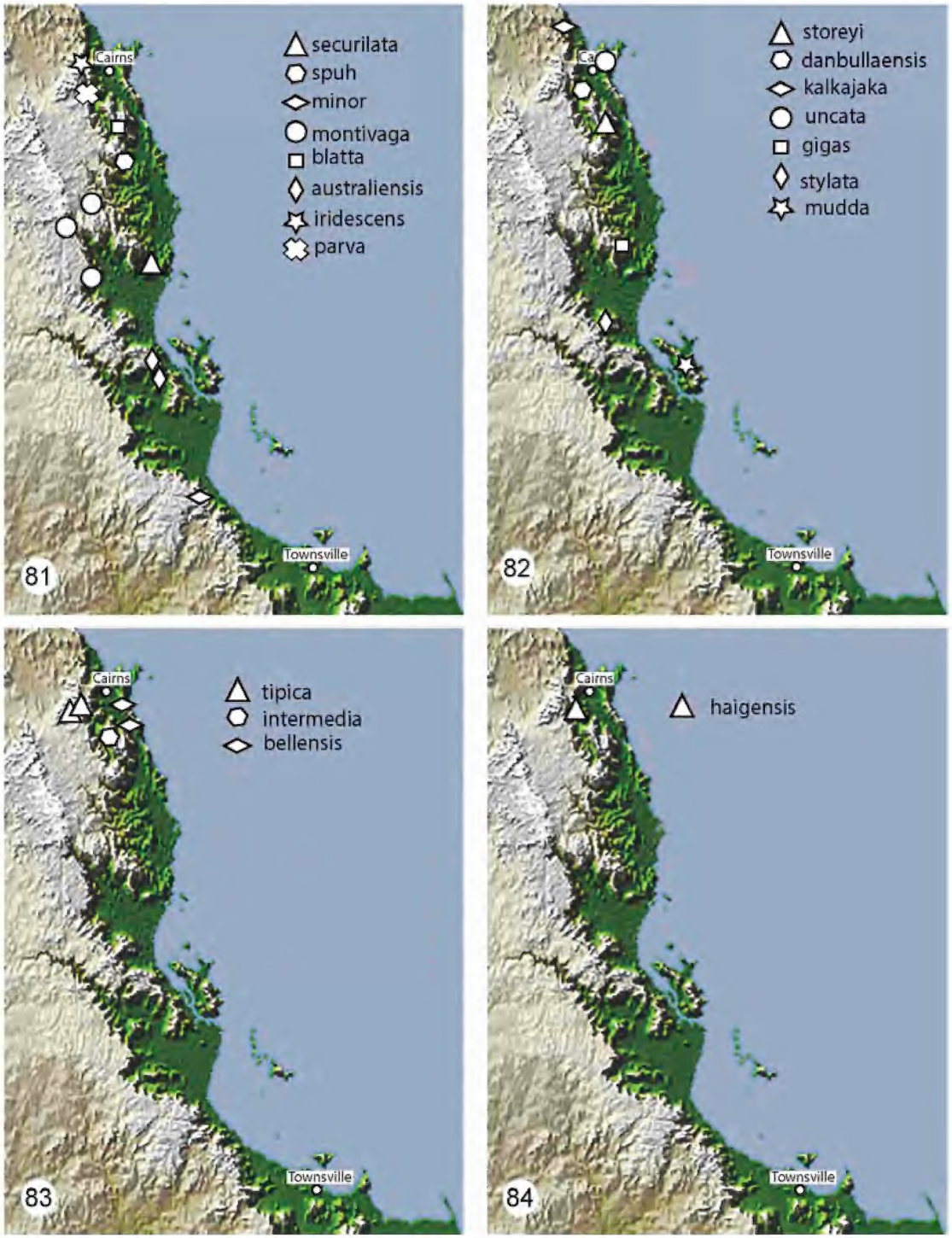
FIGS 65–70. Female reproductive tract of *Cerabilia (Feronista)* spp., ventral view. 65. *C. (F). securilata*; 66. *C. (F). montivaga*; 67. *C. (F). iridescens*; 68. *C. (F). storeyi*; 69. *C. (F). parva*; 70. *C. (F). australiensis*; bc-bursa copulatrix, bs-bursal sclerite, co- common oviduct, dl-dorsal lobe, sp- spermatheca, sg- spermathecal gland.



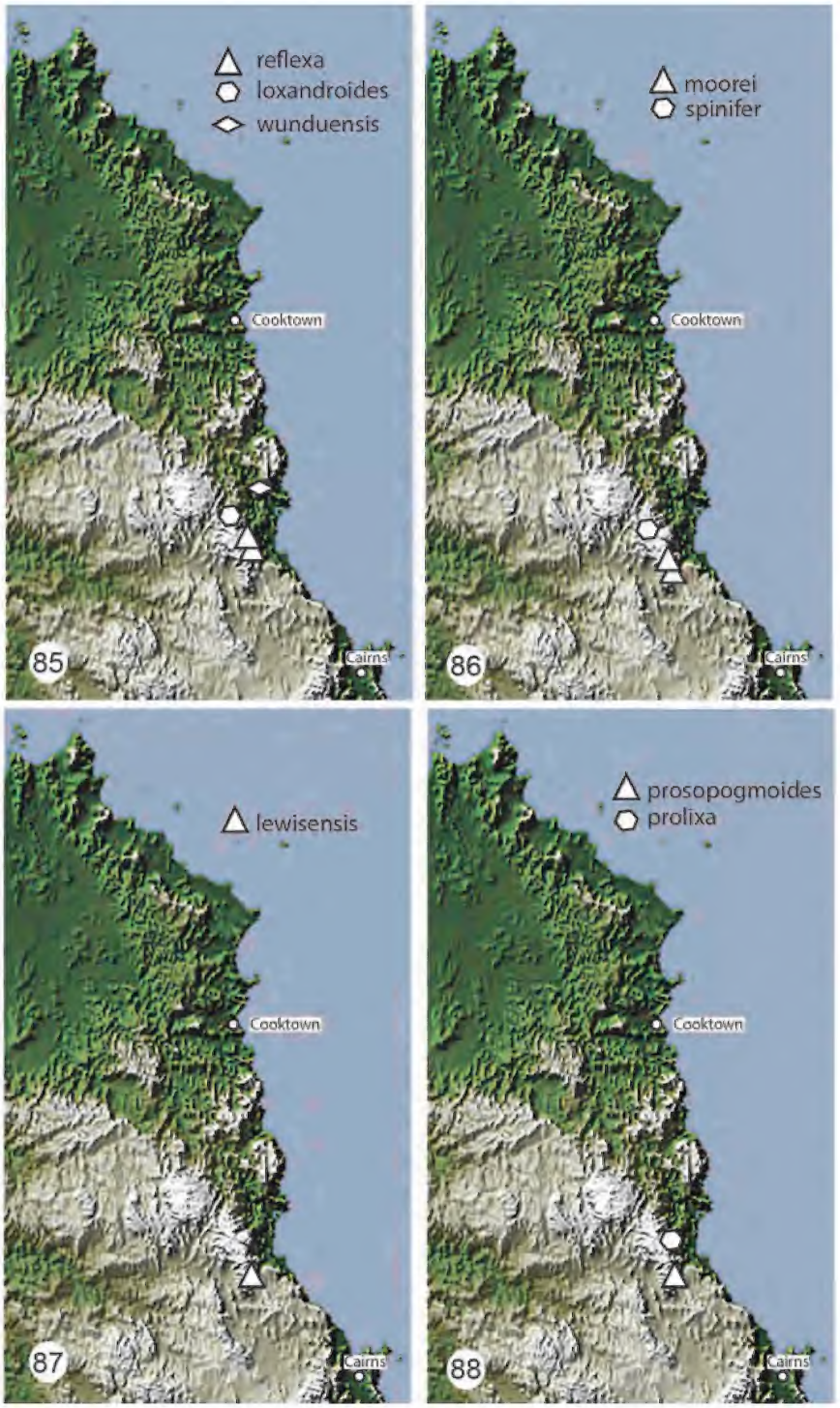
FIGS 71–74. Female reproductive tract of *Cerabilia (Feronista)* spp., 71–72,74 ventral view; 73 dorsal view. 71. *C. (F). kalkajaka*; 72. *C. (F). loxandroides*; 73–74. *C. (F). gigas*; bc-bursa copulatrix, co- common oviduct, dl-dorsal lobe, sp- spermatheca, sg- spermathecal gland.



FIGS 75–80. Female reproductive tract of *Cerabilia (Feronista)* spp., 75,77–80 ventral view; 76 dorsal view. 75–76. *C. (F). tipica*; 77. *C. (F). amaroides*; 78. *C. (F). bellensis*; 79. *C. (F). lewisensis*; 80. *C. (F). oodiformis*; bc- bursa copulatrix, co- common oviduct, dl-dorsal lobe, sp- spermatheca, sg- spermathecal gland.

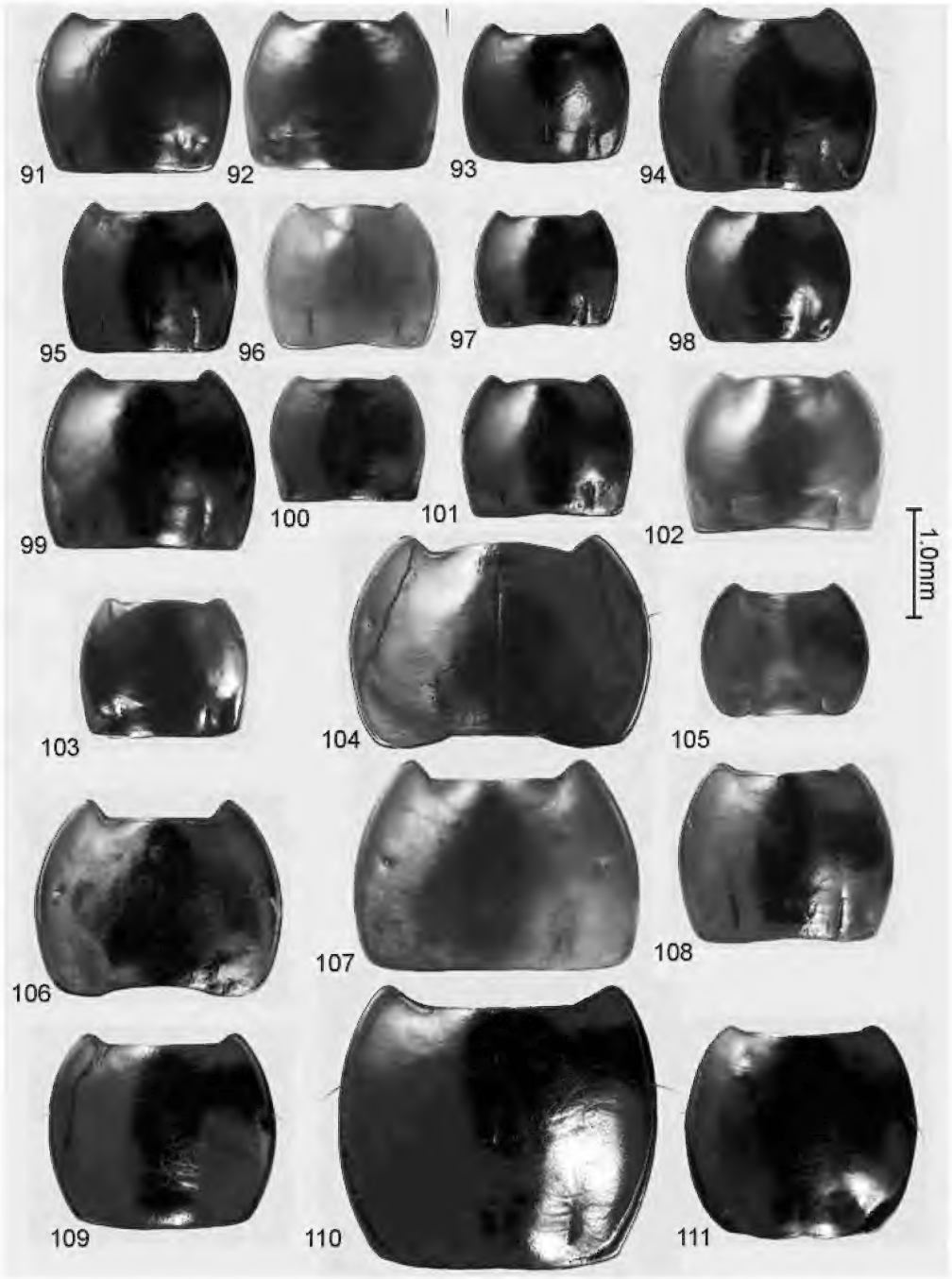


FIGS 81–84. Maps of localities for specimens of *Cerabilia (Feronista)* spp. examined.



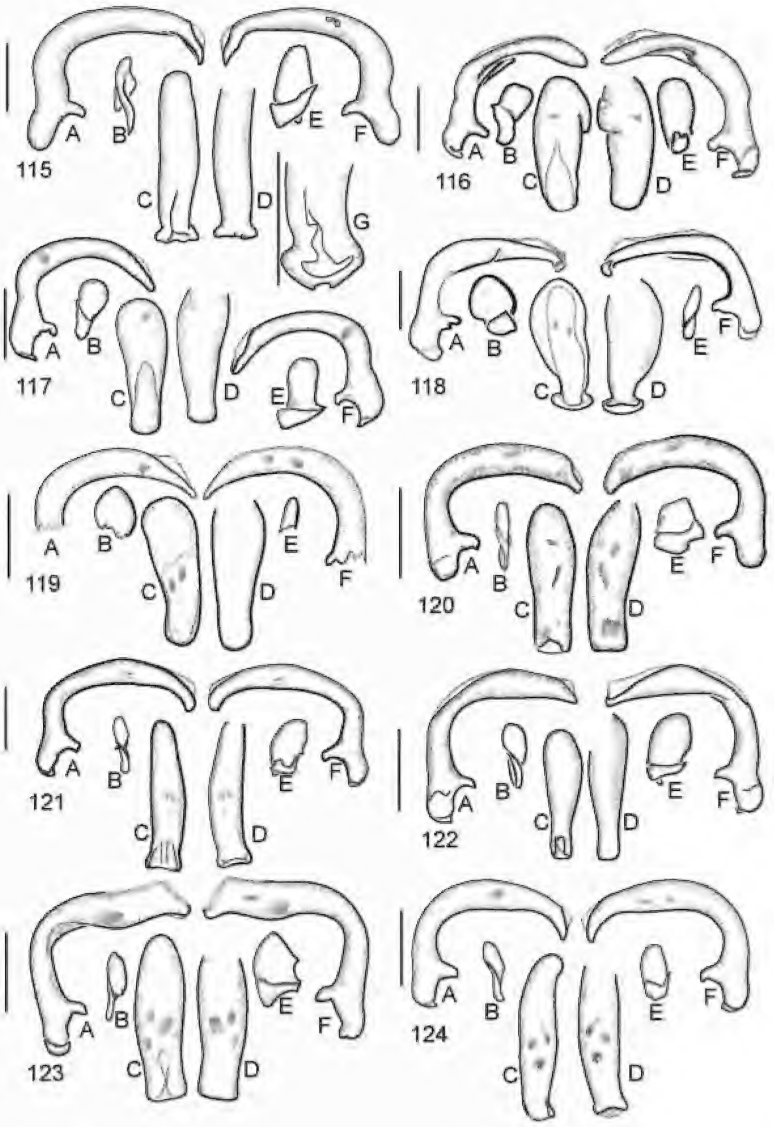
FIGS 85–88. Maps of localities for specimens of *Cerabilia (Feronista)* spp. examined.

FIGS 89–90. Maps of localities for specimens of *Cerabilia (Feronista)* spp. examined.

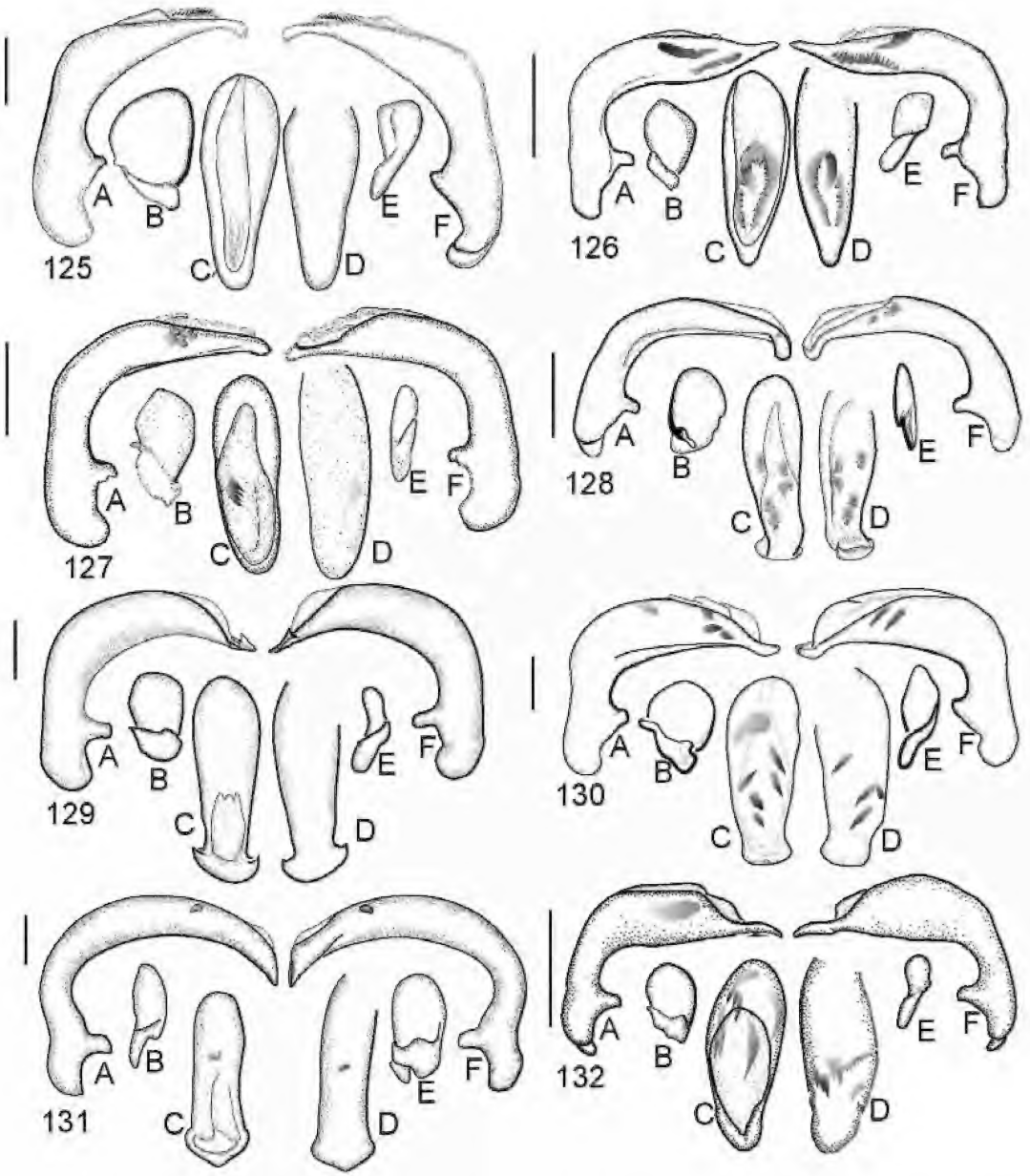


FIGS 91–111. Pronota of *Cerabilia (Biliacera)* spp., 91. *C. (B). apicesecta*; 92. *C. (B). klingonorum*; 93. *C. (B). vitalis*; 94. *C. (B). mouensis*; 95. *C. (B). kanakorum*; 96. *C. (B). rubrica*; 97. *C. (B). letalis*; 98. *C. (B). drupa*; 99. *C. (B). sternovillosa*; 100. *C. (B). paniensis*; 101. *C. (B). amieuensis*; 102. *C. (B). inversa*. 103. *C. (B). wisei*; 104. *C. (B). discosetosa*; 105. *C. (B). edentata*; 106. *C. (B). koghisensis*; 107. *C. (B). aite*; 108. *C. (B). espee*; 109. *C. (B). neocaledonica*; 110. *C. (B). francisca*; 111. *C. (B). dominatrix*.

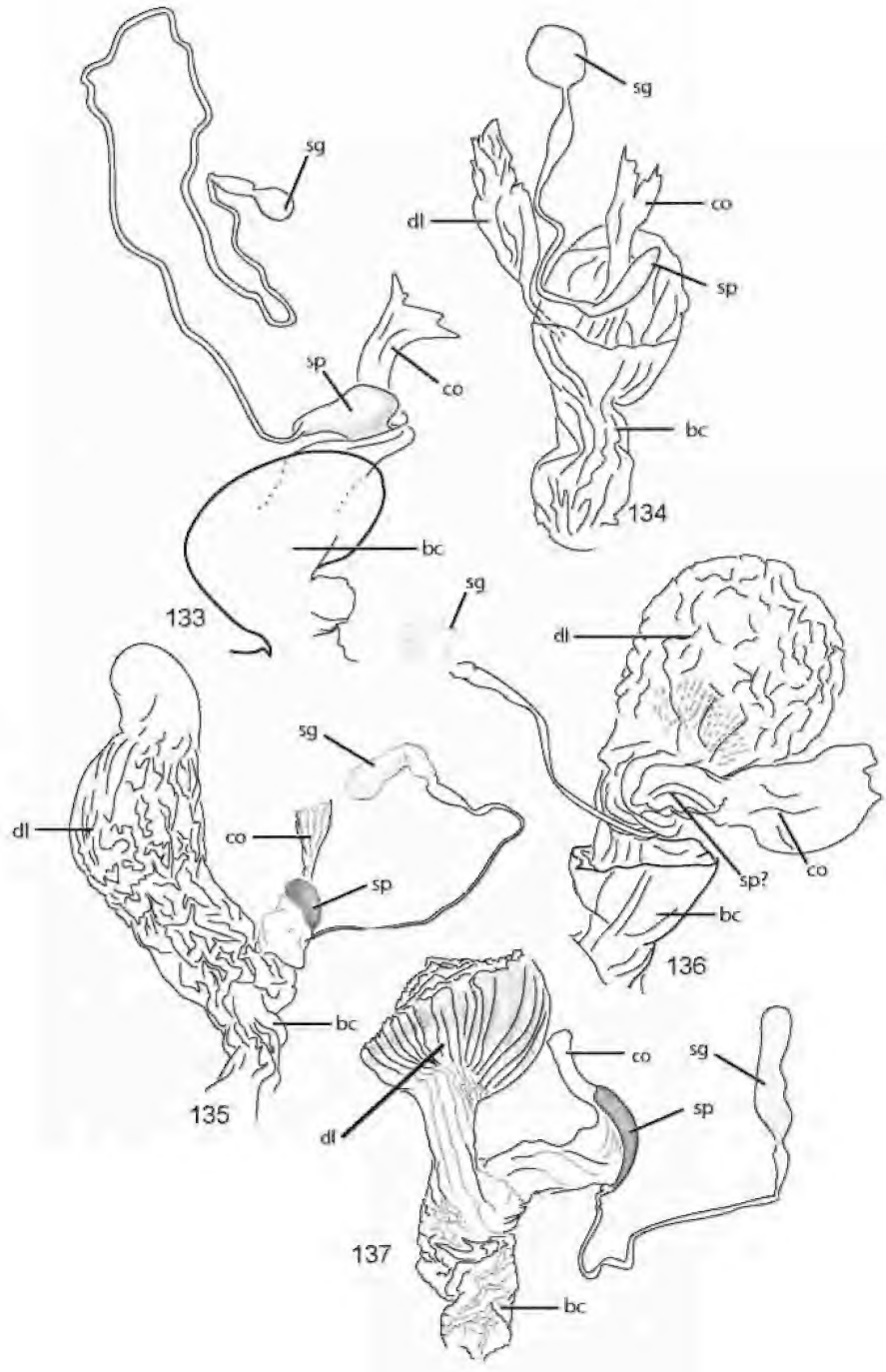
FIGS 112–114. Pronota of *Cerabilia* (*Biliacera*) spp., 112. *C. (B). ruginosa;* 113. *C. (B). orbiculata;* 114. *C. (B). nana.*



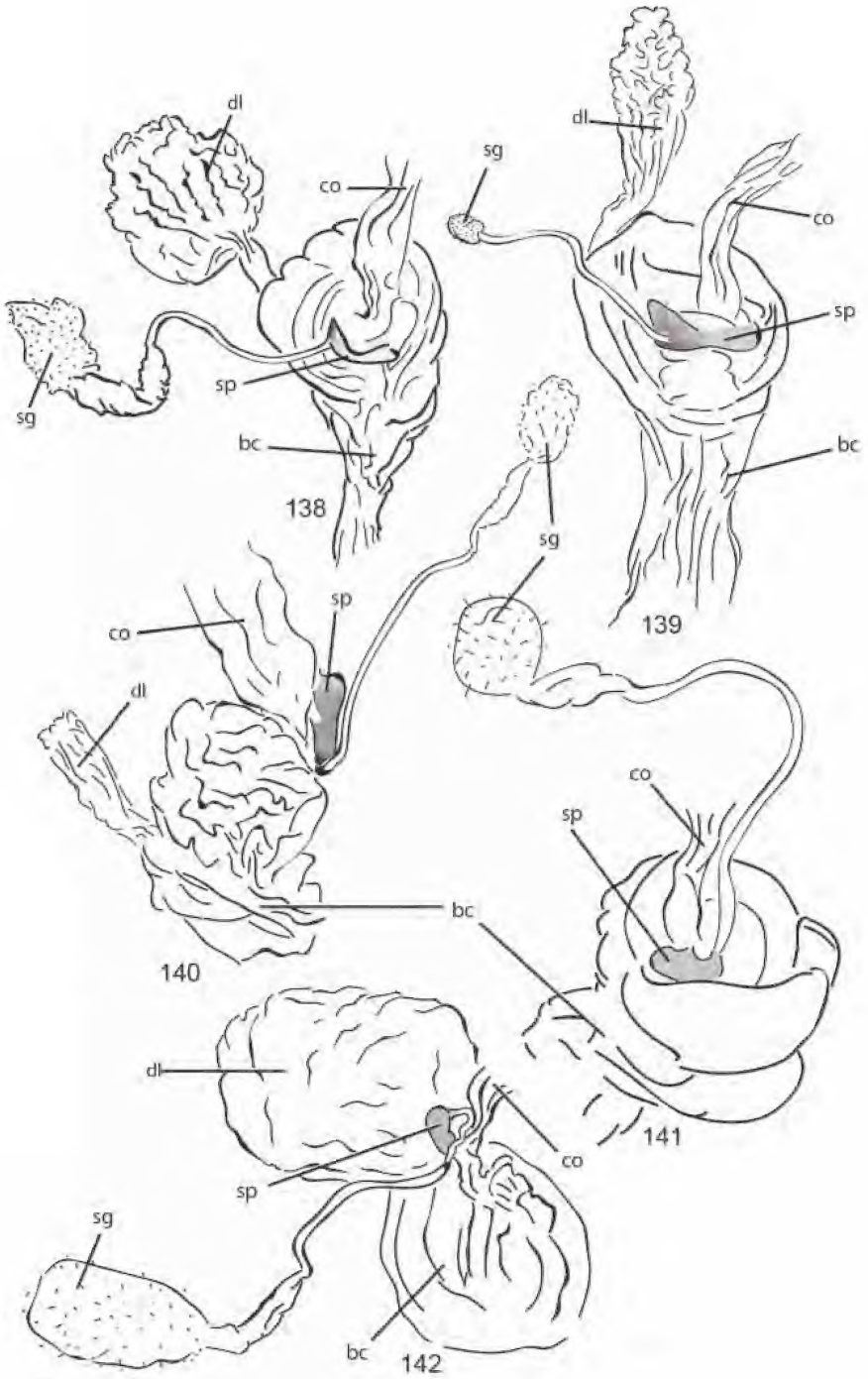
FIGS 115–124. Male aedeagus of *Cerabilia* (*Biliacera*) spp., A- left lateral, B- left paramere, C-dorsal, D-ventral, E-right paramere, F-right lateral views. Scale bars are 0.5 mm. 115. *C. (B). apicesecta;* 116. *C. (B). klingonorum;* 117. *C. (B). vitalis;* 118. *C. (B). mouensis;* 119. *C. (B). rubrica,* base of median lobe broken; 120. *C. (B). letalis;* 121. *C. (B). sternovillosa;* 122. *C. (B). amieuensis;* 123. *C. (B). inversa;* 124. *C. (B). wisei.*



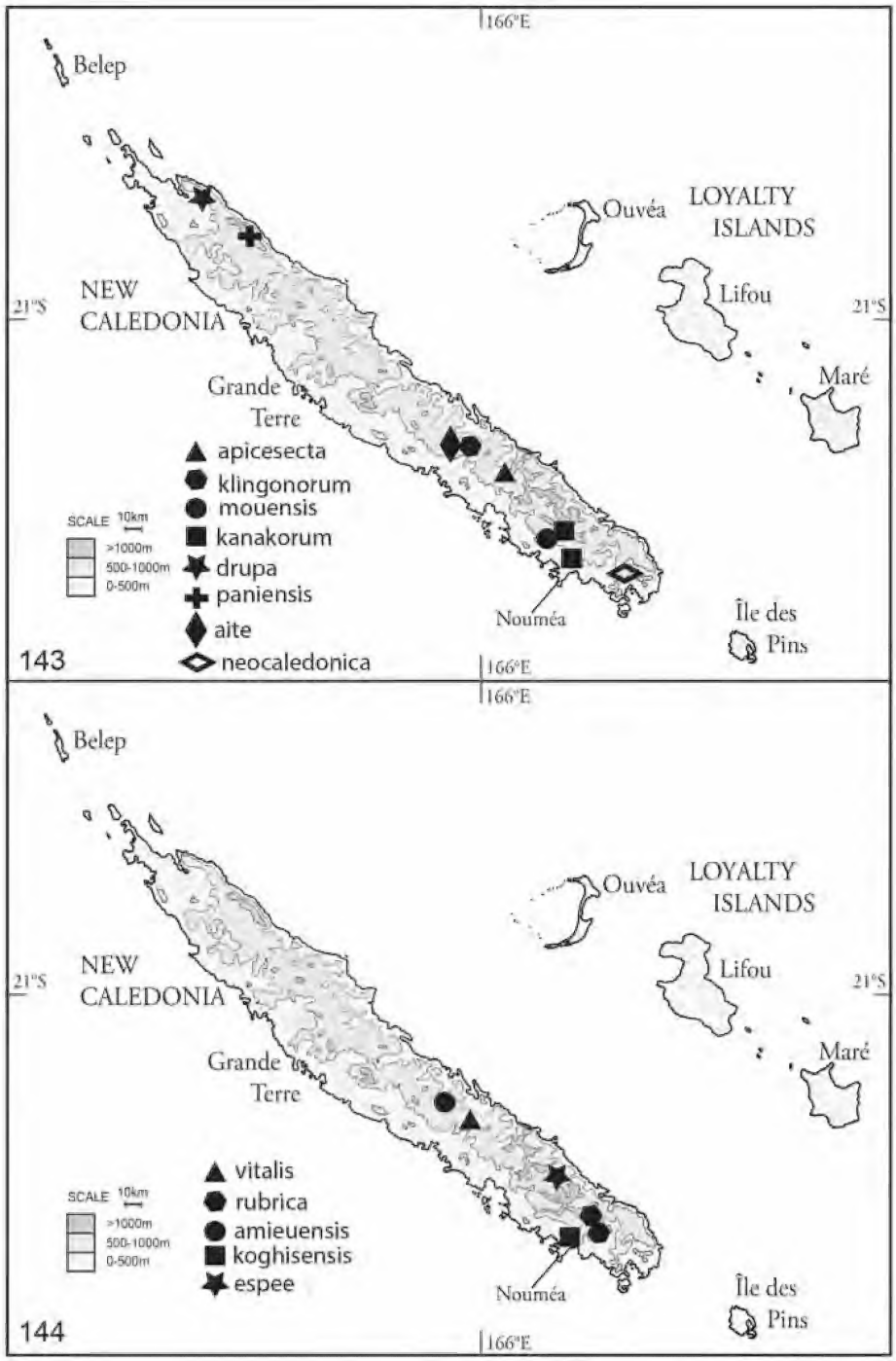
FIGS 125–132. Male aedeagus of *Cerabilia* (*Biliacera*) spp., A- left lateral, B- left paramere, C-dorsal, D-ventral, E-right paramere, F-right lateral views. Scale bars are 0.5 mm. 125. *C. (B). discosetosa;* 126. *C. (B). edentata;* 127. *C. (B). koghisensis;* 128. *C. (B). espee;* 129. *C. (B). francisca;* 130. *C. (B). dominatrix;* 131. *C. (B). ruginosa;* 132. *C. (B). nana.*



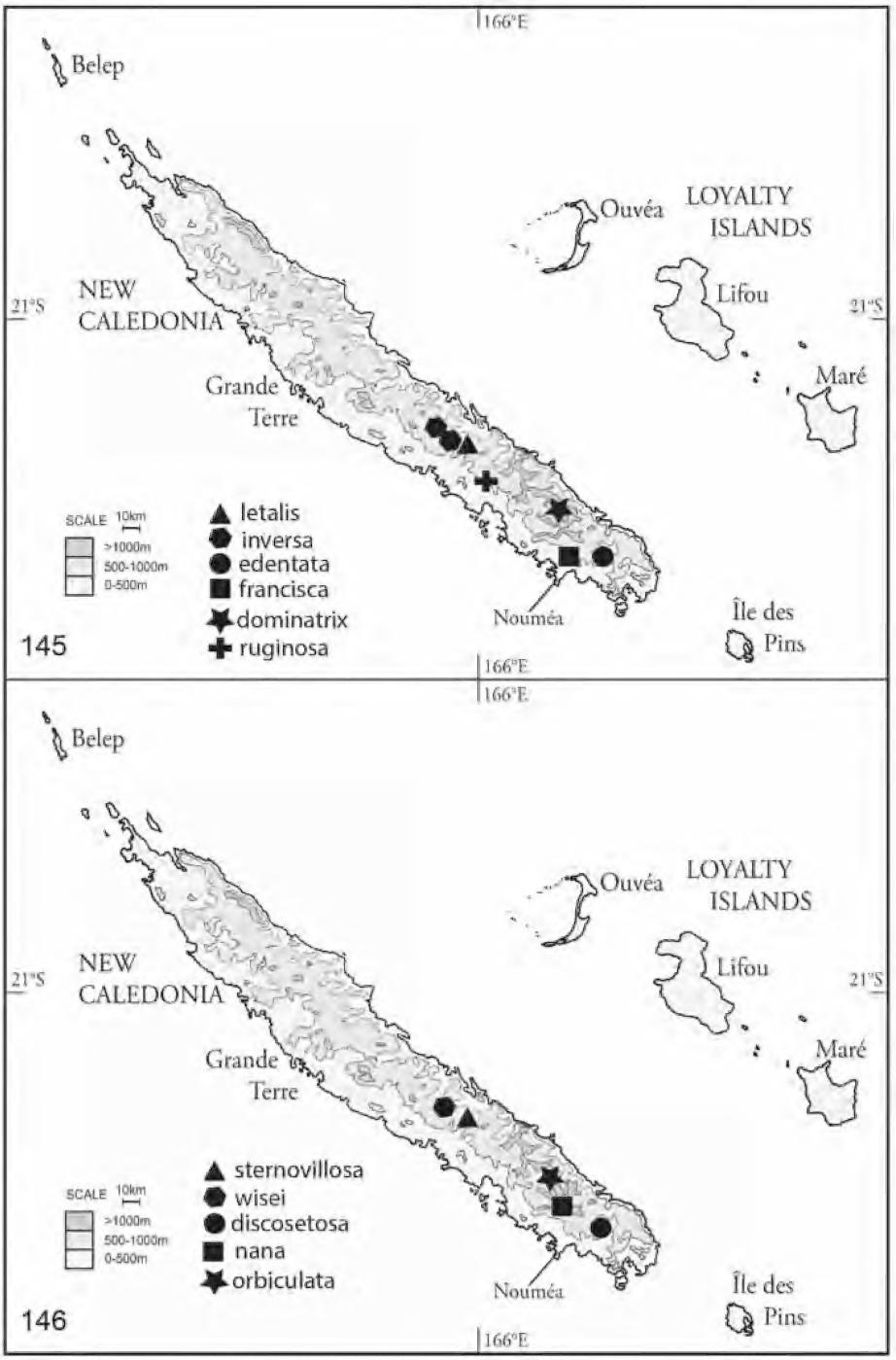
FIGS 133–137. Female reproductive tract of *Cerabilia* (*Biliacera*) spp., ventral view. 133. *C. (B). kanakorum;* 134. *C. (B). inversa;* 135. *C. (B). discosetosa;* 136. *C. (B). edentata;* 137. *C. (B). francisca*; bc-bursa copulatrix, co-common oviduct, dl-dorsal lobe, sp- spermatheca, sg- spermathecal gland.



FIGS 138–142. Female reproductive tract of *Cerabilia* (*Biliacera*) spp., ventral view. 138. *C. (B). vitalis;* 139. *C. (B). drupa;* 140. *C. (B). ruginosa;* 141. *C. (B). orbiculata;* 142. *C. (B). paniensis*; bc-bursa copulatrix, co- common oviduct, dl-dorsal lobe, sp- spermatheca, sg- spermathecal gland.



FIGS 143–144. Maps of localities for of *Cerabilia* (*Biliacera*) spp. specimens examined.



FIGS 145–146. Maps of localities for of *Cerabilia* (*Biliacera*) spp. specimens examined.

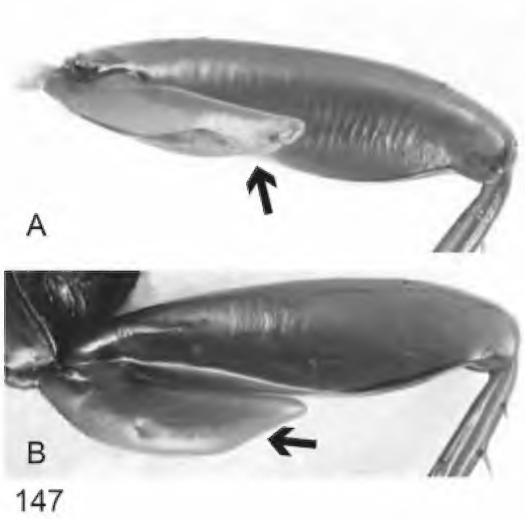


FIG. 147. Metatrochanters of *Cerabilia* (*Feronista*) *prosopogmoides*; **A**, dorsal view showing concavity; **B**, ventral view showing acuminate apex.

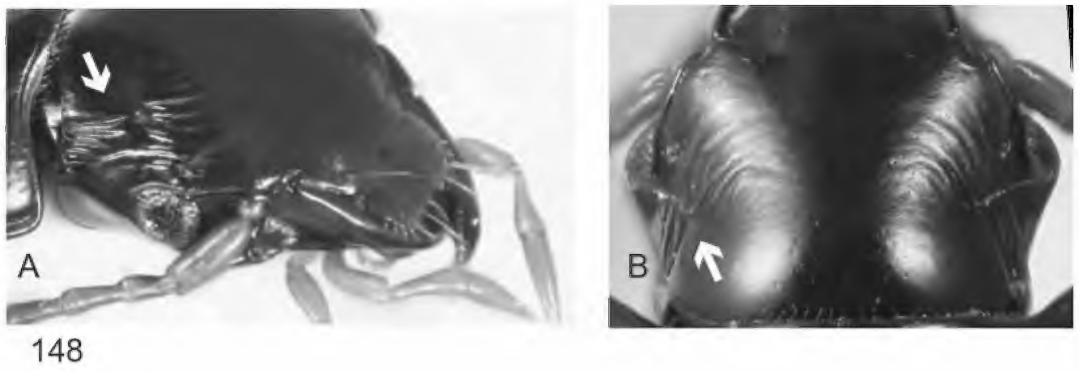


FIG. 148. Head of *Cerabilia* (*Biliacera*) *klingonorum* showing wrinkles around eyes. **A**, right lateral; **B**, dorsal views.

APPENDIX A AVAILABLE AS SUPPLEMENTARY MATERIAL ONLINE.

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Observations of 'pseudoparasitism' involving snake eels (Teleostei: Ophichthidae) in commercially important Black Jewfish *Protonibea diacanthus* (Sciaenidae) and other teleost species

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ABSTRACT

Snake eels (family Ophichthidae) are a widespread and highly diverse, but poorly understood group of fishes known worldwide in tropical to temperate waters from inshore to at least 1300 m depth. During the dissections of a commercially harvested large marine sciaenid, the Black Jewfish *Protonibea diacanthus* (Lacépède, 1802), collected from coastal waters off northern Australia, ophichthids were found encased in the mesenteries in the body cavity. Subsequently, specimens of ophichthids were also collected from the stomach contents of *P. diacanthus*, suggesting this as the potential source of the ophichthids in the body cavity. Genetic analysis confirmed four species of ophichthids were collected from the body cavity of 19 *P. diacanthus* specimens. Further investigation has revealed the occurrence of at least three additional ophichthid species from the body cavities of ten Australian teleost species classified in eight different families. Teleost species with ophichthid eels present in their guts were medium to large, opportunistic carnivores suggesting that prey items were targeted rather than incidentally ingested. Preliminary identification of the eels suggests that some may be new Australian records, highlighting an important, but little utilised source of ophichthid specimens for scientific studies. This paper presents the first published report of eels in the body cavity of fishes in Australian waters and is a good example of collaboration and co-operation on collections-based research between various stakeholders in the fisheries industry and of citizen science.

❑ *Pisces, Teleostei, Anguilliformes, Ophichthidae, pseudoparasitic, eel, marine biodiversity, northern Australia*

The family Ophichthidae, whose members are commonly known as snake eels or worm eels, is the most diverse of the true eels (Order Anguilliformes) with 351 valid species (Fricke *et al.* 2020). Snake eels are distributed in coastal, midwater and offshore waters of tropical to warm temperate oceans to at least 1300 m depth, although most species occur in less than 200 m (Smith & McCosker 1999; McCosker 2010). Snake eels are separated into two subfamilies: members of Ophichthinae (281 valid species) usually with hardened, finless tail tips and sometimes also hard, pointed snouts for burrowing tail and/or head first; and, members of Myrophinae (70 valid species) differentiated by their soft tail tips and with both dorsal and anal fin continuous with the caudal fin (Smith & McCosker 1999; Fricke *et al.* 2020). Several reports have been published of ophichthids found in the body cavities of a variety of fish species around the world (see Isbert *et al.* 2011). Reports characterised the ophichthids presence in fish body cavities as either accidental or pseudoparasitic incursions (Breder & Nigrelli 1934; Walters 1955; Garratt 1986; Isbert *et al.* 2011). Walters (1955) and Isbert *et al.* (2011) determined however, that the term 'pseudoparasite' was inappropriate and misleading, as this suggested an eel could potentially survive in the body cavity of the "host" fish. Instead, it is most likely that the snake eels were consumed as part of the fish diet, from which a small number are able to survive ingestion and enter the body cavity, where they die and become encased in the mesenteries (Walters 1955; Garratt 1986; Isbert *et al.* 2011).

The Black Jewfish, *Protonibea diacanthus* (Sciaenidae), targeted in commercial and recreational fisheries, occurs throughout tropical Indo-West Pacific marine waters; within Australia, it is found from south of Onslow (ca. 21°45'S) in Western Australia (Bray *et al.* 2012), across northern Australia, south to at least River Heads, Mary River mouth (ca. 25°25'S) on the central coast of Queensland (Barton 2018; JWJ, unpublished data). During a study on the parasites of the Black Jewfish, in northern Australian waters, specimens of snake eels were recovered from the body cavity and, subsequently, the stomach contents. Additional records of ophichthid eels in Australian teleost fishes were opportunistically collected from other sources, including museum records, research surveys and reports from recreational and commercial fishers. This paper presents data on the eels collected and discusses the potential route the eels undertook prior to encasement in the mesenteries.

MATERIALS AND METHODS

The Black Jewfish specimens reported in this study are the same as those reported in Taillebois *et al.* (2017) and Barton (2018). Fish were collected from a number of locations across northern Australia (see Taillebois *et al.* (2017) for list of all collection locations; locations where ophichthids were collected from *P. diacanthus* are listed in Table 1), primarily by line fishing by staff of both the Western Australian and Northern Territory Departments of Fisheries and Indigenous Marine Rangers as well as by commercial fishers (collected under Northern Territory Fisheries Permit S17/2737). A single ophichthid eel was also recovered from a Golden Snapper, *Lutjanus johnii* (Bloch 1792), fished from Lucinda, near Townsville, by a commercial fisher as part of the same project for which the Black Jewfish were collected. All fish were euthanased (Charles Darwin University Animal Ethics Approval A13014), placed on ice and transported to the laboratory for processing; some fishes were frozen whole prior to processing. Total length (in mm) and sex was recorded. The collection of data for stomach contents of *P. diacanthus* has been previously described in Barton (2018). Ophichthid eels removed from Crimson Snapper, *Lutjanus erythropterus* Bloch, 1790, were collected during an RV *Investigator* survey to the North-West Shelf, WA (IN2017_V05). Observations of ophichthid eels in the gut cavities of fishes from Queensland were also opportunistically collected by JWJ from a combination of personal observation and communication with recreational and commercial fishers between 1977–2013.

Specimens of eels were carefully dissected from the mesenteries in the body cavity or from the external surfaces of various organs and refrozen; specimens of eels collected from the stomach contents were also refrozen. Examination of the specimens were undertaken at CSIRO Australian National Fish Collection, Hobart. Eel specimens were identified as far as possible, based on overall morphology using Smith & McCosker (1999) with other more recent references for the family (e.g. Hibino *et al*. 2019). At least one specimen of each species retained at CSIRO was x-rayed, except for the eel specimen retrieved from a flathead collected off Newcastle, NSW; this was sent to the authors late in this study. Although the number and placement of head pores are useful taxonomic characterstics for eels, these counts were often impossible due to skin desiccation and/or abrasion from the gut of the 'host' species.

Small tissue samples from these eels were collected for genetic analysis. DNA was extracted using the Wizard® SV Genomic DNA Purification system (Promega, Australia) and as per the extraction method outlined in Nielsen *et al*. (2019). A portion of the cytochrome oxidase subunit I (COI) mitochondrial DNA gene was amplified using the BCL and BCH primers of Baldwin *et al*. (2009). Amplified products were sequenced at the CSIRO marine genetics laboratories on a 16 capillary ABI 3130XL DNA Autosequencer (Applied Biosystems™, USA) (as per amplification and sequencing protocols outlined in Appleyard *et al*. 2018). Consensus sequences were assembled in Geneious vers R8.1.4 (Biomatters Ltd, New Zealand) and compared using the BOLD IDS tool (Ratnasingham & Hebert 2007) and GenBank BLASTn (via an internal application in Geneious) to check the similarity of sample sequences against existing database reference sequences.

Institutional abbreviations follow Fricke and Eschmeyer (2020) and other abbreviations are as follows: FL = Fork Length, TL = Total Length, NSW = New South Wales, NT = Northern Territory, Qld = Queensland, WA = Western Australia. For simplicity and ease of discussion we have used the term 'host' although these eels are not truly parasitic.

RESULTS

Ophichthidae from Black Jewfish

A total of 335 *P. diacanthus* (mean TL 805.3 mm, range 330–1300 mm) collected from 13 locations across northern Australia were examined for this study; a total of 19 fish (5.6%) were found with members of the family Ophichthidae in the body cavity. Table 1 presents data for the five locations with these fish only. Table 2 presents additional data for individual fish where ophichthid incursions were investigated in further detail.

The presence of members of the family Ophichthidae is obvious at the time of dissection (Fig. 1), although the level of encasement by mesentery can differ from almost non-existent to fully encased. The level of deterioration of the specimen, with regards to usable morphological details, seemed to be related to the level of encasement by mesenteries: specimens with low encasement are presumed to have been recently ingested and were usually in much better (i.e. fresher) condition than those with high levels of encasement that are presumed to have been in the body cavity for a longer period. In addition to the presence of members of the family Ophichthidae in the mesenteries, a number of fish (four with eels in the body cavity and five without) also had eels in the stomach contents; these fish were only found in Roebuck Bay, Western Australia.

Taxonomic investigation of the eels from Black Jewfish led to them originally being identified as belonging to four different species of the family Ophichthidae based on a combination of characters including colour pattern, body depth, teeth morphology, and presence or absence of a finless, hardened tail tip. Unfortunately, due to a combination of the degraded state of the specimens and the lack of comprehensive keys to the relevant genera in the family, morphological identification of these specimens was very difficult (Table 2).

FIG. 1. Unidentified snake eels (Family Ophichthidae) found in the body cavity of *Protonibea diacanthus* in northern Australia. Arrows point to the specimen. Top left, NTM S. 17726-001 from Adelaide River, NT; bottom left and right – from Roebuck Bay, WA.

DNA analysis of eight specimens of snake eel in comparison to sequences on BOLD confirmed the presence of four different species. Despite successful sequencing, none of the specimens collected in this study were an exact (100%) pairwise match to a known species in the BOLD database.

Within the four identified species, three belong to the subfamily Ophichthinae and are most likely members of the genus *Ophichthus* Ahl, 1789; the fourth species is a member of the subfamily Myrophinae and is most likely a member of the genus *Scolecenchelys* Ogilby, 1897.

Ophichthus sp. 1 (Fig. 2A) was collected from three individuals of *P. diacanthus* from Roebuck Bay: one from the stomach (CSIRO H 8472-01) and two from the body cavity (CSIRO H 8473-01 and CSIRO H 8474-01). The three specimens had a COI gene sequence with a 98.4-98.7% match to 10 samples of "*Ophichthus* sp." from Taiwan in the BOLD database – these Taiwan specimens are likely to be *Ophichthus machidai* McCosker, Ide & Endo, 2012 (H-C. Ho, National Museum of Marine Biology & Aquarium, Taiwan, personal communication June 2019). The specimen in best condition (CSIRO H 8473-01) shares morphological similarities with *O. machidai* in having the

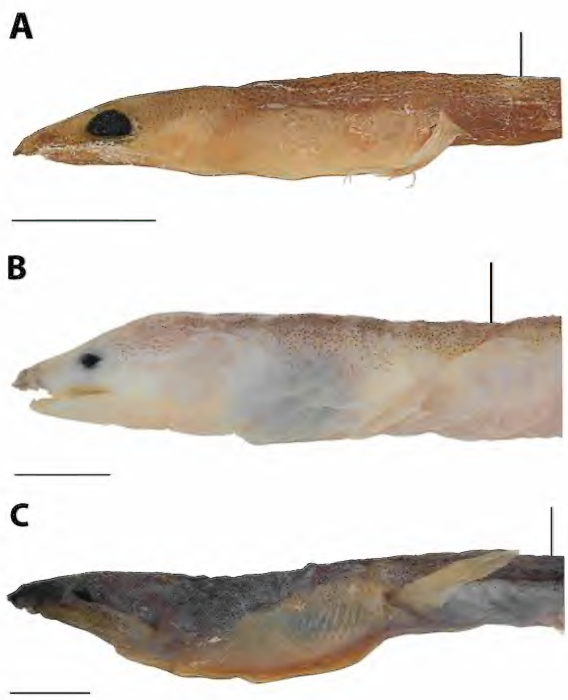

FIG. 2. Preserved lateral head images of Australian pseudoparasitic eels of genus *Ophichthus* removed from Black Jewfish, *Protonibea diacanthus*. **A**, *Ophichthus* cf. *machidai*, CSIRO H 8473-01, 140 mm TL, Roebuck Bay, WA; **B**, *Ophichthus* cf. *sangjuensis*, CSIRO H 8475-02, 198 mm TL, Roebuck Bay, WA; **C**, *Ophichthus* cf. *chilkensis*, CSIRO H 8477-02, 368 mm TL, Wyndham, WA. Vertical bars denote location of dorsal fin origin. Scale bar = 0.5 mm.

dorsal fin origin over the pectoral fin (over or slightly behind in description), elongate pectoral fins, speckled dorsal colouration and pale ventral colouration. Also, the vertebral count data (one of the key diagnostic characters for most eels) of CSIRO H 8473-01 (the only specimen x-rayed) matches the range known for *O. machidai* (i.e. ca. 12/52/150 for predorsal/preanal/total vertebrae in this specimen versus mean vertebral formula of 13/56/154 and total vertebrae 146-161 in McCosker *et al*. 2012; Hibino *et al*. 2019). However, the three Australian specimens are tentatively identified as *Ophichthus* cf. *machidai*, given that they are juveniles (140-281 mm TL versus maximum of 672 mm TL in McCosker *et al*. 2012) and the tooth and head pore morphology is difficult to determine due to either abraded skin, head missing or dehydration caused by the

TABLE 1. Locations in this study where collected *Protonibea diacanthus* included encased eel specimens of family Ophichthidae from along the coastlines of Western Australia and the Northern Territory. Locations are listed in order from west to east; only locations with encased fish are listed.

Location	No. fish	Mean mm TL (Range)	Number of fish encased (%)	Mean intensity of fish encasement (%)
Western Australia				
Roebuck Bay	36	1018.5 (720-1199)	13 (36.1)	1.54 (1-3)
Kimberley	20	646.7 (520-920)	2 (10)	1
Wyndham	34	1067.1 (804-1300)	2 (5.9)	1.5 (1-2)
Northern Territory				
Cape Hotham	10	990 (430-1230)	1 (10)	1
Maningrida	29	730.9 (420-1210)	1 (3.4)	1
TOTAL	129	906.8 (420-1300)	19 (14.7)	1.4 (1-3)

Eel taxon	Museum Reg. No.	Size (mm TL)	BOLD No.	Host family	Host species	Host size (mm TL)	Host organ	Host collection locality	Approximate position	Date host collected
Ophichthus cf. *machidai*	CSIRO H 8472-01	281	BW-A13816	Sciaenidae	*P. diacanthus*	1012 mm	stomach	WA, Roebuck Bay	18°04'S, 122°15'E	7/08/2015
Ophichthus cf. *machidai*	CSIRO H 8473-01	140	BW-A13817	Sciaenidae	*P. diacanthus*	980 mm	mesenteries	WA, Roebuck Bay	18°04'S, 122°15'E	31/07/2015
Ophichthus cf. *machidai*	CSIRO H 8474-01	>172	BW-A13818*	Sciaenidae	*P. diacanthus*	1010 mm	mesenteries	WA, Roebuck Bay	18°04'S, 122°15'E	1/08/2014
Ophichthus cf. *machidai*	CSIRO H 8474-01	212	BW-A13819	Sciaenidae	*P. diacanthus*	1010 mm	mesenteries	WA, Roebuck Bay	18°04'S, 122°15'E	1/08/2014
Ophichthus cf. *sanguiensis*	CSIRO H 8475-01	213	BW-A13821	Sciaenidae	*P. diacanthus*	1100 mm	stomach	WA, Roebuck Bay	18°04'S, 122°15'E	21/06/2015
Ophichthus cf. *sanguiensis*	CSIRO H 8475-02	198	BW-A13822	Sciaenidae	*P. diacanthus*	1100 mm	stomach	WA, Roebuck Bay	18°04'S, 122°15'E	21/06/2015
Ophichthus cf. *chilkensis*	CSIRO H 8477-01	>260	BW-A13823	Sciaenidae	*P. diacanthus*	822 mm	mesenteries	WA, Cambridge Gulf	15°28'S, 128°06'E	1/05/2015
Ophichthus cf. *chilkensis*	CSIRO H 8477-02	368	BW-A13824	Sciaenidae	*P. diacanthus*	822 mm	mesenteries	WA, Cambridge Gulf	15°28'S, 128°06'E	1/05/2015
Scoleocnchelys sp.	CSIRO H 8476-01	>150	BW-A13815	Sciaenidae	*P. diacanthus*	870 mm	stomach	WA, Roebuck Bay	18°04'S, 122°15'E	14/08/2015
Ophichthinae	NTM S.17726-001	205	BW-A12762*	Sciaenidae	*P. diacanthus*	1230 mm	swimbladder	NT, the Narrows	12°14'S, 131°16'E	25/04/2014
Ophichthinae	NTM S.17727-001	2.72-160	No DNA	Sciaenidae	*P. diacanthus*	649 mm	swimbladder	WA, Three Ways Creek	16°12'S, 124°33'E	4/10/2014
Ophichthinae	NTM S.16084-001	245	No DNA	Sciaenidae	*P. diacanthus*	not recorded	body cavity	NT, Chambers Bay	12°13'S, 131°35'E	15/06/2005
Ophichthinae	NTM S.18451-001	ca. 177	No DNA	Sciaenidae	*P. diacanthus*	not recorded	body cavity	NT, Off Bynoe Harbour	12°23'S, 130°18'E	15/08/2005
Ophichthinae	NTM S.16558-001	124	No DNA	Sciaenidae	*P. diacanthus*	not recorded	body cavity	NT, Chambers Bay	12°13'S, 131°35'E	May 2007
Ophichthinae	NTM S.16503-001	158	No DNA	Sciaenidae	*P. diacanthus*	not recorded	body cavity	NT, Charles Pt	12°19'S, 130°39'E	June 2007
Yirrkala cf. *chaselingi*	CSIRO H 8292-27	355	BW-A15141	Lutjanidae	*Lutjanus erythropterus*	ca. 500-590	mesenteries	WA, north of Cape Lambert	20°12'S, 117°22'E	20/10/2017
Ophichthinae	CSIRO unregistered	145	No DNA	Lutjanidae	*Lutjanus johnii*	785	mesenteries	Qld, Lucinda	18°32'S, 146°20'E	25/05/2014
Malvoliophis pinguis	not retained	unknown	No DNA	Pomatomidae	*Pomatomus saltatrix*	not recorded	body cavity	Qld, Scarborough	27°11'S, 153°07'E	May 1977
Leiuranus semicinctus	not retained	ca. 285	No DNA	Scombridae	*Acanthocybium solandri*	1475 mm FL, 22.3 kg	body cavity	Qld, off Cairns	17°15'S, 147°30'E	30/09/2011
Ophichthinae	not retained	?	No DNA	Serranidae	*Hyporthodus ergastularius*	not recorded	body cavity	Qld, Fraser I to Gold coast	ca. 24°S - 28°S	26/11/2013
Ophichthinae	not retained	?	No DNA	Serranidae	*Hyporthodus octofasciatus*	not recorded	body cavity	Qld, Fraser I to Gold coast	ca. 24°S - 28°S	26/11/2013
Ophichthinae	not retained	?	No DNA	Polyprionidae	*Polyprion oxygeneios*	not recorded	body cavity	Qld, Fraser I to Gold coast	ca. 24°S - 28°S	26/11/2013
Ophichthinae	not retained	?	No DNA	Centrolophidae	*Hyperoglyphe antarctica*	not recorded	body cavity	Qld, Fraser I to Gold coast	ca. 24°S - 28°S	26/11/2013
Ophichthinae	CSIRO unregistered	ca. 120	Not yet sampled	Platycephalidae	*Platycephalus richardsoni*	not recorded	body cavity	NSW, Newcastle region	32°56'S, 151°47'E	2019

TABLE 2. Records of pseudoparasitic eels referred to in this study (> denotes damaged due to head missing; * denotes sequencing attempted, but unsuccessful). Ophichthinae refers to specimens that are currently unresolved beyond subfamily level due to dessication and/or damage.

gut cavity. As *O. machidai* has not yet been confirmed from Australia (McCosker *et al.* 2018; previously only documented from Japan and Taiwan by Hibino *et al.* 2019), we defer conclusive identification of these specimens until material in better condition becomes available. Kimura *et al.* (2018) also noted two un-named *Ophichthus* species from Vietnam which share similar features with this unknown species from northern Australia.

Ophichthus sp. 2 (Fig. 2B) was collected from the stomach of a single, large *P. diacanthus* female at Roebuck Bay; two specimens (CSIRO H 8475-01 and CSIRO H 8475-02) were examined in detail and subsampled for genetics. When compared with other sequences in the BOLD database, *Ophichthus* sp. 2 showed 94.3–94.5% similarity to two specimens of *Ophichthus brevicaudatus* Chu, Wu & Jin 1981 from China. Slightly more divergent (93.5–94.0% similarity) to these sequences was a sequence from another undetermined species of *Ophichthus* or *Pisodonophis* Kaup, 1856 from Indonesia, Philippines and Taiwan. *Ophichthus* sp. 2 has minute melanophore-sized spots dorsally and is pale ventrally with the dorsal fin origin above the anterior to middle of pectoral fin and with three to five premaxillary teeth visible when mouth closed. Vertebral count data collected from one of the two specimens was 12/48/143, which is close to *Ophichthus sangjuensis* (Ji & Kim 2011) with MVF 14/50/147 and total vertebrae range 143–153 (Hibino *et al.* 2019). Again, as this species has not been recorded from Australia, we tentatively identified it as *Ophichthus* cf. *sangjuensis*, pending confirmation of its existence in Australia from specimens in better condition and larger size (these two Australian specimens are 198–213 mm TL, but it is documented to 627 mm TL by Ji & Kim 2011).

Two specimens of *Ophichthus* sp. 3 (CSIRO H 8477-01; H 8477-02, Fig. 2C) were collected from the mesenteries of a single *P. diacanthus* from Wyndham. The sequences from both specimens were grouped together (although there is a base pair variation between the two COI sequences) and showed 87.9-89.1% similarity with *Pisodonophis boro* (Hamilton 1822), from India (type locality), Bangladesh and China, and 86.2–86.8% similarity to an unresolved taxon, *Pisodonophis* sp. (NTM S.17851-011) from Joseph Bonaparte Gulf, WA. The genera *Pisodonophis* and *Ophichthus* are currently inadequately defined (Hibino *et al.* 2019), so both genera are relevant to the identification of this unknown species. The two specimens are very elongate and bicolored, darker dorsally than ventrally. Only one (CSIRO H 8477-02) of the two specimens is completely intact (CSIRO H 8477-01 is missing the head, presumably damaged when extracted), so taxonomic characters discussed are limited to CSIRO H 8477-02. Both jaws have irregularly biserial (mostly recurved) teeth, the vomerine teeth are biserial for most of their length (longer anteriorly), 7 premaxillary teeth are present, the anterior nostrils are tubular and located on the upper lip, and a small barbel is present between the anterior and posterior nostrils. The eyes are very small, head length is 16.8 times in TL (approx. 6% TL), tail length 66.2% TL, head length 5.6 times in Trunk Length. The dorsal fin origin is just behind the rear tip of the pectoral fin (by about half length of pectoral fin) and the pectoral fin base is restricted to the dorsal half of the gill opening. The vertebral count of 13/65/209 is at the upper limits for most ophichthid species but most closely matches *Ophichthus chilkensis* Chaudhuri, 1916, currently known only from India (Mishra *et al.* 2019). Given that the generic limits for *Ophichthus* and *Pisodonophis* are uncertain, and the large range extension that this would be, it is tentatively identified as *Ophichthus* cf. *chilkensis* until further specimens from Australia or matching genetic sequences from India can be confirmed.

A single specimen of subfamily Myrophinae (CSIRO H 8476-01, not figured) was collected from the stomach of a *P. diacanthus* from Roebuck Bay. The COI sequence from this specimen showed a 93.9–94.0 % similarity with a sequence from *Scolecenchelys macroptera* (Bleeker, 1857) collected from China. The single specimen was unfortunately missing its head so limited morphological data could be collected. Although an unknown number of anterior

vertebrae are missing, it is clear that the dorsal fin origin is nine vertebrae in advance of the anal fin origin, the total vertebrae less pre-anal vertebrae count is 88 and the total vertebrae less pre-dorsal vertebrae count is 97. Although it is difficult to assign this species to a taxon with the limited data available, we tentatively refer it to *Scolecenchelys* sp., although it is perhaps possible that it could also belong to genus *Muraenichthys* Bleeker, 1853 or another Myrophine genus if the *S. macroptera* sequence in BOLD has been misidentified.

Some previous 'pseudoparasitic' eel samples collected from the body cavity of *P. diacanthus* by NT Fisheries and commercial fishers and lodged with NTM are also included in Table 1. These specimens were in relatively poor condition without DNA samples, so identifications are lacking at this stage.

Eels from other teleost fishes

Ophichthidae from Golden Snapper. A single ophichthid specimen was collected from the mesenteries of a Golden Snapper, *Lutjanus johnii*, sampled at Lucinda, north Qld. The specimen was very degraded / digested and morphological examination could not identify it further than to the family. Molecular analysis was not attempted.

Ophichthidae from Crimson Snapper. In November 2017, during an RV *Investigator* voyage off the North West Shelf of WA, three specimens of ophichthid eels were removed from the mesenteries of a Crimson Snapper, *Lutjanus erythropterus* (Chris Dowling, Fisheries WA, personal communication July 2019). The specimens were relatively intact, and a COI sequence was obtained for the specimen in best condition (CSIRO H 8292-27, Fig. 3). This sequence shared 91.0 % similarity with *Callechelys catostoma* (Schneider, 1801) from French Polynesia and 90.1-90.2 % similarity with *Yirrkala tenuis* (Günther, 1870) from the Seychelles. The vertebral count of the three specimens (ca. 7-8 predorsal, ca. 79-81 preanal and ca. 149-153 total) and the absence of pectoral fins is a close match to two species of *Yirrkala* known from northern Australia, namely *Yirrkala chaselingi* Whitley, 1940 with ca. 150-155 vertebrae, and *Yirrkala calyptra* McCosker, 2011 with 7-9/73-75/143-147 vertebrae (McCosker, 2011). The overlapping distribution of *Y. chaselingi* (the other two Australian *Yirrkala* species are currently only known from Qld; see McCosker *et al.* 2018) points to it being the most likely candidate, but comparative pre-dorsal and pre-anal vertebral counts and certainty over the true number of supraorbital pores is lacking (McCosker 2011 noted 'appears to have three rather than four supraorbital pores', but the best specimen we examined has four). *Yirrkala ori* McCosker, 2011, known from South Africa, also has 4 supraorbital pores and a similar vertebral count, i.e. 6-7/71-76/149-152 (McCosker, 2011). We tentatively identify this specimen as *Yirrkala* cf. *chaselingi* until a more definitive description of the species is provided.

Ophichthidae from other Australian teleosts in Queensland

Since 1977, JWJ has collated records of instances in Qld where ophichthid eels were discovered in the body cavities of another five teleost fishes in four different families collected by recreational and commercial fishers. The first was a live Halfband Snake Eel, *Malvoliophis pinguis* (Günther 1872), inside the body cavity of a Tailor, *Pomatomus saltatrix* (Linnaeus 1766) (Pomatomidae) from Moreton Bay (JWJ, unpublished data, specimen not retained or photographed). The second was an encased Saddled Snake Eel, *Leiuranus semicinctus* (Lay & Bennett 1839), inside a Wahoo, *Acanthocybium solandri* (Cuvier 1832) (Scombridae) collected by longline off Cairns (M. Zischke, personal communication to JWJ, Fig. 4, specimen not retained), the eel identification evident from the 25 broad dark saddles (narrowest across head) interspersed by narrow white bars (see Randall 2005). Lastly, unidentified ophichthid species (specimens photographed but not retained) were collected from depths of 300-500 m by a commercial fisher around seamounts in south-east Qld between Fraser Island and the Gold Coast from four different

FIG. 3. Preserved lateral head image of *Yirrkala* cf. *chaselingi* (CSIRO H 8292-27, 355 mm TL, North of Cape Lambert, WA) removed from Crimson Snapper, *Lutjanus erythropterus*. Vertical bar denotes location of dorsal fin origin. Scale bar = 0.5 mm.

teleost species in three different families (J. Rowley, personal communication to JWJ). These additional teleosts include what was previously and colloquially known as 'bar cod' (now known to consist of Banded Rockcod *Hyporthodus ergastularius* (Whitley 1930) and Eightbar Grouper, *Hyporthodus octofasciatus* (Griffin 1926), family Serranidae), Hapuku (*Polyprion oxygeneios* (Schneider & Forster 1801), family Polyprionidae) and Blue-eye Trevalla (*Hyperoglyphe antarctica* (Carmichael 1819), family Centrolophidae).

Ophichthidae from NSW Tiger Flathead. Lastly, in late 2019 just prior to the submission of this manuscript, a specimen of unidentified Ophichthidae was extracted from the body cavity of a Tiger Flathead (*Platycephalus richardsoni* Castelnau 1872, family Platycephalidae). The specimen was originally caught by a commercial fisher off Newcastle, NSW and purchased from the Sydney Fish Markets. It is small (ca. 120 mm TL) and the tail tip is damaged, making genus identification difficult, but dorsal and anal fins are present and pectoral fins appear to be absent. Extraction of DNA has not yet been attempted.

DISCUSSION

This study represents the first report of the presence of encased snake eels in a number of fishes in Australian waters. Within the family Ophichthidae, members of the genera *Ophichthus*, *Myrichthys* Girard, 1859 and *Apterichtus* Duméril, 1805 have been reported from the body cavities of various fish species, ranging from the Bahamas, Florida, the north-west Atlantic to the Mediterranean Sea (Isbert *et al*. 2011); members of the genera *Callechelys* Kaup, 1856 and *Caecula* Vahl, 1794 were also found in a variety of fishes from South Africa (Garratt 1986). All the "host" fish reported were predatory, and most had a benthic habitat preference (see Waters 1955); three of the fish reported belonged to the family Serranidae (see Isbert *et al*. 2011) which have a similar ecology to the family Sciaenidae, to which *P. diacanthus* belongs. Interestingly,

FIG. 4. Fresh dorsal image of *Leiuranus semicinctus* from Wahoo, *Acanthocybium solandri*. Specimen not retained, ca. 285 mm TL, east of Cairns, Qld. Image by M. Zischke. Scale bar = 1 cm.

coincident with the study on *P. diacanthus*, a similar study was undertaken on a number of other fish species (families Lutjanidae and Lethrinidae) from the same collection locations; only one *Lutjanus johnii* out of 1200 specimens of mixed species examined, all predatory, but not specifically benthic, were found to have encased eels (Barton, unpub. data), although the eel genus could not be identified. A second benthic snapper species, *Lutjanus erythropterus,* was recently found with an encased eel, genus *Yirrkala* from the North West Shelf, WA. Other host families encountered during this study (Platycephalidae, Polyprionidae, Serranidae) are primarily benthic to benthopelagic in nature, although some (e.g. Centrolophidae, Scombridae) can also be associated with seamounts and drop-offs and have pelagic aspects to their behaviour, likely driven by diurnal and /or nocturnal vertical migrations for feeding. It is difficult to know if all the eels were taken near the benthos as there are also some pelagic members of the Ophichthidae, including *Neenchelys* Bamber, 1915 (Ho *et al.* 2015), but some eels were unidentifiable either due to poor condition or not being retained.

It is most likely that snake eels form a small part of the diet of these opportunistic predators, from which a small number are able to survive the ingestion and are then able to enter the body cavity in which they die and become encased in the mesenteries (Walters 1955; Garratt 1986; Isbert *et al.* 2011). This is supported by the collection of a number of eels collected from stomach contents of *P. diacanthus* in this study (see Barton 2018). Further, the fact that there was 100% COI genetic similarity between *Ophichthus* cf. *machidai* collected from the stomach (CSIRO H 8472-01) and from the mesenteries (CSIRO H 8473-01) of an individual *P. diacanthus*, confirms the relationship. During dissections of *P. diacanthus*, occasional wounds were found in the stomach wall, presumed to have been caused by the spines of teleosts such as fork-tailed catfishes (family Ariidae, which were common dietary items in specimens from Wyndham), but possibly also stingrays (family Dasyatidae), or fish hooks; representatives of all three were found in the body cavity of *P. diacanthus* during the study. Snake eels normally exist in burrows in the sand and routinely reverse or dive into soft substrate using their hard, pointed head or tail tip. If snake eels were ingested by a jewfish with a wounded stomach wall, they could potentially burrow out of the stomach via the wound into the body cavity, whereby they die and become encased in the mesenteries. However, the pointed head and /or tail tip of snake eels likely facilitates ease of burrowing through the soft stomach lining, even in the absence of damage to the stomach lining. Fishes that burrow into sediments (infaunal) are presumably tolerant

of low oxygen environments and could feasibly stay alive for longer inside the gut cavities of species that predate upon them, once ingested.

Although not a parasite, the presence of these eels in the jewfish were sufficient to be utilised as a biological tag in Taillebois *et al.* (2017). Presence of these eels was high in comparison to previous reports, although it should be noted that very few studies have previously documented their frequency. Isbert *et al.* (2011) found snake eel specimens entangled in the mesenteries of 1 out of 45 pandoras (*Pagellus erythrinus* (Linnaeus, 1758); Sparidae) in the Mediterranean Sea, with a further 2 pandoras having eels in the stomachs. Garratt (1986) examined over 9000 sparids and serranids and found 11 individuals with an encased eel in the body cavity; only one eel was found per fish.

Larson *et al.* (2013) reported 18 species of Ophichthidae from waters of the Northern Territory, Australia. A number of these species were reported to also occur in Asia and other waters off the coast of northern Australia. Of the species that were close to the "species" identified in this study *S. macroptera* and *Pisodonophis boro* also occurred in Australian waters. However, several species listed by Larson *et al.* (2013) are not represented by a COI sequence in the BOLD database, so whether the eels found in the stomachs and body cavities of *P. diacanthus* in this study belong to these species remains unknown. There are several shallow-water northern Australian ophichthids that are yet to be conclusively identified (J. McCosker personal communication March 2013 in Larson *et al.* 2013). Further collections of eels from the body cavities of fishes in Australian waters needs to be undertaken with specimens utilised for genetic and morphological analysis. Unfortunately, the biodiversity of snake eels in northern Australia is inadequately documented and as discussed it is possible that some of these specimens represent new Australian records or are undescribed species.

This study has built upon previously published reports and highlights that at least seven species of pseudoparasitic ophichthid eels in five genera are recorded from ten different species of Australian teleost fishes in eight families, namely Centrolophidae, Lutjanidae, Platycephalidae, Polyprionidae, Pomatomidae, Serranidae, Sciaenidae and Scombridae. The broad depth range of the host species (inshore to around 500 m) suggests that numerous more species of ophichthid eels could be recorded in this fashion, so it is clear that the diversity of both the pseudoparasitic eels and their hosts will expand as researchers become more aware of this little-known phenomenon. This study also highlights a positive outcome from collaboration and co-operation on collections-based research between various stakeholders in the fisheries industry and of citizen science.

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Alastair Graham (CSIRO, Hobart) assisted with specimen registration and data acquisition and Narissa Bax (CSIRO, Hobart) photographed and etched images of preserved specimens. Glenn Moore (Western Australian Museum, Perth) and Chris Dowling (Fisheries WA, Perth) both provided data on the Western Australian distribution of *P. diacanthus* and Chris Dowling removed ophichthid eel specimens from Crimson Snapper (*Lutjanus erythropterus*), during stomach content analysis onboard IN2017_V05. Md. Shafaet Hossen (Charles Sturt University, Wagga Wagga) dissected and retained an ophichthid specimen from the flathead *Platycephalus richardsoni* collected off Newcastle, NSW.

LITERATURE CITED

Appleyard, S.A., White, W.T., Vieira, S. & Sabub, B. 2018. Artisanal shark fishing in Milne Bay Province, Papua New Guinea: biomass estimation from genetically identified shark and ray fins. *Scientific Reports* 8, **6693**: 1–12. https://doi.org/10.1038/s41598-018-25101-8

Baldwin, C.C., Mounts, J.H., Smith, D.G. & Weigt, L.A. 2009. Genetic identification and colour descriptions of early life-history stages of Belizean Phaeoptyx and *Astrapogon* (Teleostei: Apogonidae) with comments on identification of adult *Phaeoptyx*. *Zootaxa* **2008**: 1–22.

Barton, D.P. 2018. Notes on the diet of the black-spotted croaker (*Protonibea diacanthus*) across northern Australia. *Northern Territory Naturalist* **28**: 61-69.

Bray, D.J., Hoese, D.F., Paxton, J.R. & Lockett, M.M. 2012. Sciaenidae. Australian Faunal Directory. Australian Biological Resources Study, Canberra. Available from: https://biodiversity.org.au/afd/taxa/SCIAENIDAE Accessed 7 Oct, 2019.

Breder, A.M. Jr. & Nigrelli, R.F. 1934. The penetration of a grouper's digestive tract by a sharp-tailed eel. *Copeia* **1934**: 162-164. https://doi.org/10.2307/1435846

Fricke, R. & Eschmeyer, W.N. 2020. *Eschmeyer's Catalog of Fishes: Guide to Fish Collections.* http://researcharchive.calacademy.org/research/ichthyology/catalog/collections.asp Electronic version accessed 06 Feb 2020.

Fricke, R., Eschmeyer, W.N. & Fong, J.D. 2020. Eschmeyer's Catalog of Fishes: Species by Family / Subfamily. http://researcharchive.calacademy.org/research/Ichthyology/catalog/SpeciesByFamily.asp Electronic version accessed 20 Mar 2020.

Garratt, P.A. 1986. Ophichthid eels in the coelom of several Natal offshore reef fish. *South African Journal of Zoology* **21**: 274-275. https://doi.org/10.1080/02541858.1986.11447996

Hibino, Y., McCosker, J.E. & Tashiro, F. 2019. Four new deepwater *Ophichthus* (Anguilliformes: Ophichthidae) from Japan with a redescription of *Ophichthus pallens* (Richardson 1848). *Ichthyological Research* **66**(2): 289-306. https://doi.org/10.1007/s10228-018-00677-3

Ho, H.-C., McCosker, J.E. & Smith, D.G. 2015. Renaming of three recently described eels of the genus *Neenchelys* (Teleostei: Anguilliformes: Ophichthidae) from the western Pacific. *Zootaxa* **4060**: 49-51. https://dx.doi.org/10.11646/zootaxa.4060.1.7

Isbert, W., Montero, F.E., Fernández, M., Lombarte, A., Sacanell, M. & Orejas, C. 2011. Ophichthids (Ophichthidae: Anguilliformes) within the body cavity of marine fishes: pseudoparasites? *Marine Biodiversity Records* **4**: e33. https://doi.org/10.1017/S1755267211000285

Ji, H.-S. & Kim, J.-K. 2011. A new species of snake eel, *Pisodonophis sangjuensis* (Anguilliformes: Ophichthidae) from Korea. *Zootaxa 2758: 57-68.* http://dx.doi.org/10.11646/zootaxa.2758.1.4

Kimura, S., Imamura, H., Nguyen, V.Q. & Pham, T.D. 2018. *Fishes of Ha Long Bay, the natural world heritage site in northern Vietnam*. Fisheries Research Laboratory, Mie University, Shima Japan. ix + 314 pp.

Larson, H.K., Williams, R.S. & Hammer, M.P. 2013. An annotated checklist of the fishes of the Northern Territory, Australia. *Zootaxa* **3696**: 1-293. http://dx.doi.org/10.11646/zootaxa.3696.1.1

Mishra, S.S., Mohapatra, A., Ray, D., Mohanty, S.R. & Tudu, P.C. 2019. *Ophichthus chilkensis* Chaudhuri, 1916 (Anguilliformes: Ophichthidae) - resurrection as a valid species from India, with re-description. *Zootaxa* **4586**: 194-200. https://doi.org/10.11646/zootaxa.4586.1.13

McCosker, J.E. 2010. Deepwater Indo-Pacific species of the snake-eel genus *Ophichthus* (Anguilliformes: Ophichthidae), with the description of nine new species. *Zootaxa* **2505**: 1-39. https://doi.org/10.11646/zootaxa.2505.1.1

McCosker, J.E. 2011. Two new Indo-Pacific species of the sand-eel genus Yirrkala (Anguilliformes: Ophichthidae). *Smithiana Publications in Aquatic Biodiversity Bulletin* **13**: 45-50.

McCosker, J. E., Ide, S. & Endo, H. 2012. Three new species of ophichthid eels (Anguilliformes: Ophichthidae) from Japan. *Bulletin of the National Museum of Nature and Science* (Ser. A) Supplement No. 6: 1-16.

McCosker, J.E, Allen, G.R., Hoese, D.F., Lockett, M.M, Gates, J.E. & Bray, D.J. 2018. Ophichthidae. Australian Faunal Directory. Australian

Biological Resources Study, Canberra. Available from: https://biodiversity.org.au/afd/taxa/OPHICHTHIDAE. (Accessed 7 Oct, 2019)

Nielsen, J.G., Pogonoski, J.J., Appleyard, S.A. 2019. Aphyonid-clade species of Australia (Teleostei, Bythitidae) with four species new to Australian waters and a new species of *Barathronus*. *Zootaxa* **4564**: 554-572. https://doi.org/10.11646/zootaxa.4564.2.12

Ratnasingham, S. & Hebert, P.D.N. 2007. http://www.barcodinglife.org. BOLD: The barcode of life data system. *Molecular Ecology* **7**: 355–364.

Randall, J.E. 2005. *Reef and shore fishes of the South Pacific. New Caledonia to Tahiti and the Pitcairn Islands*. University of Hawai'i Press, Honolulu. i-xii + 1-707.

Smith, D.G. & McCosker, J.E. 1999. Family Ophichthidae. Pp. 1662-1669. *In,* Carpenter, K.E & Niem, V.H. (eds) Species identification guide for fisheries purposes. *The living marine resources of the western central Pacific. Batoid fishes, chimeras and bony fishes part 1* (Elopidae to Linophrynidae). (FAO, Rome. v. 3: iii-vi + 1398-2068, I-IV).

Taillebois, L., Barton, D.P., Crook, D.A., Saunders, T., Taylor, J., Hearnden, M., Saunders, R.J., Newman, S.J., Travers, M.J., Welch, D.J., Greig, A., Dudgeon, C., Maher, S. & Ovenden, J.R. 2017. Strong population structure deduced from genetics, otolith chemistry and parasite abundances explains vulnerability to localized fishery collapse in a large Sciaenid fish, *Protonibea diacanthus*. *Evolutionary Applications* **10**: 978-993. https://doi.org/10.1111/eva.12499

Walters, V. (1955) Snake-eels as pseudoparasites of fishes. *Copeia*. **1955**: 146-147. https://doi.org/10.2307/1439338

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Planthoppers (Insecta: Hemiptera: Fulgoromorpha: Fulgoroidea: Surijokocixiidae) of the Queensland Triassic

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ABSTRACT

The suborder Fulgoromorpha, highly diverse and speciose today, was a minor component of the Cicadomorpha-dominant hemipteran fauna of the Queensland Triassic known only from five tegmen specimens of three species in three genera of the extinct family Surijokocixiidae: *Tricrosbia minuta* Evans, 1971, and *Crosbixius carsburgi* gen. et sp. nov., from the Late Triassic (Norian) Mount Crosby Formation of the Ipswich Coal Measures, and *Karesmina punicea* gen. et sp. nov. from the Middle Triassic (Anisian) Esk Formation. The Surijokocixiidae are otherwise known from four Permian genera from Russia and unnamed Triassic species from Kyrgyzstan and China. *Tricrosbia* Evans, 1971, is distinguished from other genera of the family by its simple MP1+2, and the very shallow fork of CuA. *Crosbixius* is similar to the Permian *Surijokocixius* Becker-Migdisova, but differs in the costal space of equal width along its entire length, the more basal fork of ScP+RA and RP, and mp-cu running between MP and CuA1 rather than MP3+4 and CuA1. *Karesmina* is distinguished by its larger size (tegmen length 9 mm, < 6 mm in the others), backwardly inclined ir, and peculiar structure of RP and MP1+2. *Tricrosbia* and *Crosbixius* were the last of the Surijokocixiidae which were extinct by the end of the Triassic, succeeded in the Jurassic by a more diverse and modern looking fulgoromorph fauna, dominated by numerous species of the extinct Fulgoridiidae. Confirmation of the presence of the Surijokocixiidae in the Mount Crosby Formation adds another family to the Ipswich Coal Measures hemipteran fauna, a transition insect fauna typical of the Triassic, with a mix of survivors from the Permian which did not last beyond the Triassic (Dunstaniidae, Scytinopteridae, Surijokocixiidae) or Jurassic (Dysmorphoptilidae), peculiar Triassic endemics (Chiliocyclidae, Mesogereonidae, Ipsviciidae), the newly emerged Hylicellidae which survived until the Cretaceous, and lastly more modern forms, Archijassidae, the earliest record of the extant Membracoidea, and Tettigarctidae, the hairy cicadas, which still exist today.

❑ *Insecta, Hemiptera, Fulgoromorpha, Fulgoroidea, Surijokocixiidae, Tricrosbia, Mount Crosby Formation, Esk Formation, fossil insects.*

Triassic sedimentary formations of south-eastern Queensland have yielded a numerous and diverse hemipteran fauna comprising Cicadomorpha (including Scytinopteroidea), Sternorrhyncha and Heteroptera (Jell 2004). Thus far however, just one specimen has been recorded of the diminutive *Tricrosbia minuta* Evans, 1971, the only representative of the highly diverse extant suborder Fulgoromorpha, the planthoppers (Szwedo 2018). Through patient and persistent field work at two Triassic fossil insect sites in south-eastern Queensland, local enthusiast Allan Carsburg has collected three additional fulgoromorph tegmen specimens – a second specimen of *T. minuta* and a specimen of an undescribed species from the Mount

Crosby Formation, and a specimen of another undescribed species from the Esk Formation. A search of the collections of the Queensland Museum has also revealed a second specimen of the same undescribed Mount Crosby species. The two new species are described, and *T. minuta* is redescribed herein.

The three species belong to the extinct fulgoromorph family Surijokocixiidae, established by Shcherbakov (2000) for the Permian *Surijokocixius* Becker-Migdisova, 1961, *Scytocixius* Martynov, 1937, *Boreocixius* Becker-Migdisova, 1955, (Russia) and the Triassic *Tricrosbia* Evans, 1971, (Queensland). Shcherbakov (2016) added the Russian Permian *Paraprys* Aristov and Rasnitsyn, 2014, to the family's inventory; unnamed specimens of the family have also been recorded from the Triassic of Kyrgyzstan (Shcherbakov 2011) and China (Zheng *et al*. 2018). The surijokocixiids were quite small plant-hoppers, with tegmina usually less than 6 mm long, the new Esk species being the exception at about 9 mm. The family is characterised by a tegmen 'usually coriaceous with membrane smooth, costal area broad, precostal carina wide, C slightly angulate near base, R and CuA deeply forked, M at least twice forked, *cup-pcu* absent, Pcu+A1 joining claval suture' (Shcherbakov 2004). While the fulgoromorph affinities of the Surijokocixiidae are generally accepted, there are different views on its position within the Fulgoromorpha. Shcherbakov (1996, 2004, 2016) has proposed placement of Surijokocixiidae in the Fulgoroidea, as that superfamily's most primitive family, arguing that these 'Permian [and Triassic] planthoppers are already cixiid-like, similar to living ones enough to be included in Fulgoroidea' (Shcherbakov 2004). On the other hand, Szwedo *et al*. (2004), Bourgoin and Szwedo (2008) and Szwedo (2018) have proposed that the family is sufficiently distinct to warrant allocation to its own fulgoromorph superfamily, Surijokocixioidea, separate from the Fulgoroidea. The superfamily classification of Shcherbakov (1996, 2004, 2016) has been adopted herein.

THE FOSSIL LOCALITIES

The four Mount Crosby Formation specimens examined herein were collected at Mount Crosby Fossil Insect Localityies; locality B, a water pipeline cutting near Allawah Road, at -27.552° 152.782°, and Locality C, a gully running into the Brisbane River, at -27.550° 152.769° (details in Tindale 1945, Allen 1961). The two localities are in the vicinity of the suburb of Mount Crosby, approximately 10 km north of the town of Ipswich in south-eastern Queensland.The Mount Crosby Formation lies near the base of the Ipswich Coal Measures (Purdy and Cranfield 2013) which have been dated as Late Triassic (Norian) (Raven *et al*. 2015). The Esk Formation fossil insect site is in pinkish siltstone of the Middle Triassic (Anisian) Esk Formation (Purdy 2013) exposed near 5 Mile Creek on the western shore of Lake Wivenhoe in south-eastern Queensland, at -27.309° 152.521°. The only ones described thus far are a species of Titanoptera (Jell & Lambkin 1992), and two insects Hemiptera: Scytinopteridae (Lambkin 2016).

MATERIALS AND METHODS

All specimens examined are single tegmina. Specimens with both part and counterpart have an a/b number, otherwise only the part is present. The length was measured from the base of R to the apex of the tegmen, and the width from the costal margin in a perpendicular line to the apex of the clavus. Venational and other tegminal terminology follows that of Bourgoin *et al*. (2015), including the use of the term 'peripheral membrane' for the 'special and very narrow marginal area, extending from the nodus to the apex of the clavus' (Bourgoin *et. al.* 2015). The only exception is that I have used the term precostal carina for the ventrally-expressed carina along the costal margin and converging with it near the node (Shcherbakov 2016). The abbreviations used are as follows: bc, basal cell; pc, precostal carina; pm, peripheral membrane; ScP, subcosta posterior; R, radius; RA, radius anterior; RP, radius posterior; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; ir, crossvein between RA

and RP; rp-mp, crossvein between RP and MP; mp-cua, crossvein between MP and CuA; C1a, apical cell between ScP and RA.

The photographs were focus-stacked with Zerene Stacker software from source images taken with a Canon 5S camera on a Visionary Digital BK-Plus Lab System. For ease of comparison all specimens are illustrated as right tegmina. The original photographs of left tegmen specimens have therefore been mirrored, as indicated in the figure captions. All specimens are in the collection of the Queensland Museum, with designation QMF.

SYSTEMATICS

ORDER Hemiptera Linnaeus, 1758

SUBORDER Fulgoromorpha Evans, 1946

SUPERFAMILY Fulgoroidea Latreille, 1807

FAMILY Surijokocixiidae Shcherbakov, 2000

Tricrosbia Evans, 1971

Tricrosbia Evans, 1971: 145; Hamilton, 1992: 428; Shcherbakov, 2000: 251; Jell, 2004: 64; Szwedo *et al.*, 2004: 41.

Type species. *Tricrosbia minuta* Evans, 1971, by original designation.

Emended diagnosis. Tegmen small, less than 4 mm long, *c.* 2 times longer than wide; costal and apical margins evenly rounded; costal margin and ScP+R→ScP+RA more or less parallel, costal space therefore of equal width for entire length; fork of ScP and RA distal to level of primary MP fork; ScP and RA entering antero-apical margin; ScP more or less upright, RA slightly concave, the cell between them (C1a of Bourgoin *et al.* 2015) narrowly triangular; fork of ScP+RA and RP slightly proximal to ½ tegmen length, about midway between basal cell and fork of ScP and RA; RP with 2 branches, directed towards apical margin; *ir* not detected; one *rp-mp*, upright, between RP and MP1+2 ; MP1+2 simple, MP3+4 with 2 or 3 branches; *mp-cua* between MP3+4 and CuA1; CuA shallowly forked, nearly at apex of clavus, at same level as primary MP fork, with 2 short, more or less straight parallel branches, directed towards postero-apical margin.

Notes. The diagnosis is based on an analysis of the descriptions and figures of three of the previously described genera of the family, *Surijokocixius*, *Scytocixius* and *Boreocixius* (Martynov 1937, Rohdendorf *et al.* 1961, Becker-Migdisova 1962) The fourth genus, *Parapryg*, is too poorly preserved and documented to be included in the analysis (Shcherbakov 2016). *Tricrosbia* is clearly distinct from the three genera in the position of the fork of ScP+RA and RP (much more distal in *Surijokocixius* and *Scytocixius*, but much more basal (just beyond basal cell) in *Boreocixius*), the simple MP1+2 (at least 2-branched in the others), and the very shallow fork of CuA, at the same level as the primary MP fork (much deeper in the others, at around ½ tegmen length, far basal to the primary MP fork). Additionally it differs from *Surijokocixius* in the costal space of equal width over its entire length rather than expanded basally, the much smaller C1a cell, and the more or less straight branches of CuA (strongly curved posteriorly in *Surijokocixius*); from *Scytocixius* in the much smaller C1a cell; and from *Boreocixius* in ScP and RA entering the antero-apical rather than the anterior margin, RP with 2 rather than 3 branches, the presence of *rp-mp*, and the more or less straight branches of CuA (at least CuA1 strongly curved in *Boreocixius*).

Tricrosbia was considered by Evans (1971) as Fulgoroidea, by Hamilton (1992) as Cicadomorpha: Hylicellidae, and by Jell (2004) as Fulgoridae. Shcherbakov (2000) agreed with Evans on the fulgoroid affinities of the genus and included it in his newly established family Surijokocixiidae within the Fulgoroidea. Szwedo *et al.* (2004) listed *Tricrosbia* under Surijokocixiidae, and with Bourgon and Szwedo (2008) and Szwedo (2018) placed the family in its own fulgoromorph superfamily, Surijokocixioidea.

Tricrosbia minuta Evans, 1971
(Fig. 1)

Tricrosbia minuta Evans, 1971: 267; Jell, 2004: 64, one unnumbered fig.; Lambkin, 2019a: 392–393.

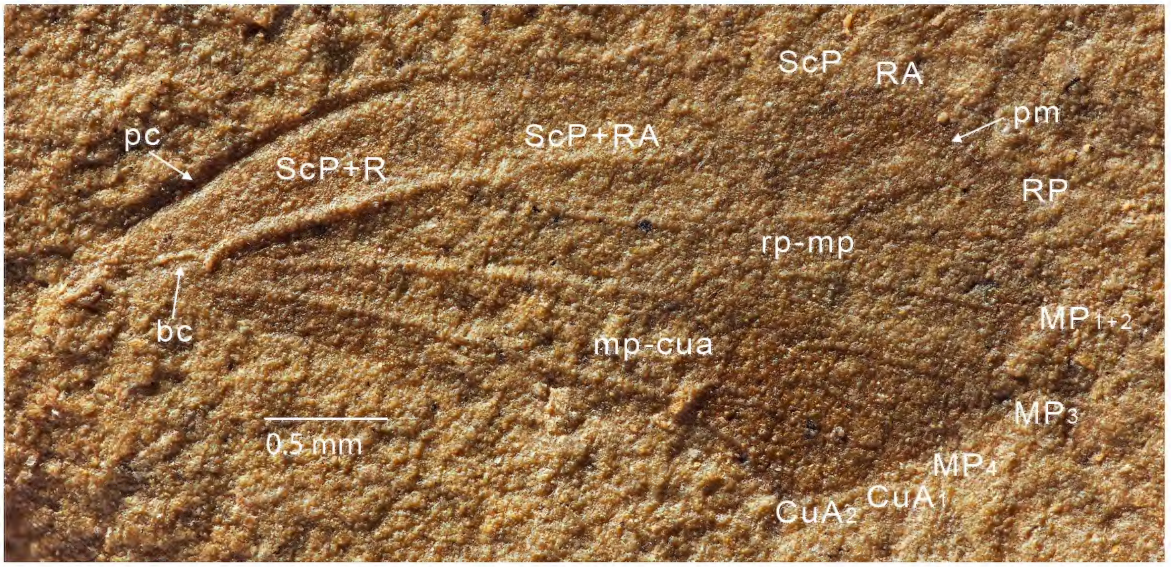

FIG. 1. *Tricrosbia minuta* Evans, 1971, QMF60132. bc, basal cell; pc, precostal carina; pm, peripheral membrane.

Material examined. Holotype tegmen QMF6520, Mount Crosby Formation, Fossil Insect Locality C. One other tegmen, QMF60132, Mount Crosby Formation, Fossil Insect Locality B, collected by Allan Carsburg. Late Triassic (Norian).

Description. Tegmen 3.4 (holotype), 3.8 mm long, 1.8 mm wide (only measurable in QMF60132); MP3+4 with 2 branches in QMF60132, 3 in holotype; clavus preserved in holotype only, Pcu+A1 directed towards apex; typical fulgoroid post-nodal peripheral membrane clearly developed; membrane (post-nodal area of tegmen) darkly shaded, corium pale.

Notes. Evans' holotype tegmen is fairly well preserved, and even though it has a glob of resin covering the antero-medial area, much of the marginal venation is still visible. In considering Evans' illustration (Evans 1971, fig. 1), however, it should be noted that the base of the tegmen is not preserved, and that neither the oblique inter-radial crossvein, nor the long crossvein between MP and CuA could be detected in the present study.

Crosbixius gen. nov.

Type species. *Crosbixius carsburgi* sp. nov.

Etymology. The generic name, which is masculine, is a combination of 'Crosb' from Mount Crosby, and 'ixius', part of the standard generic root 'cixius'.

Diagnosis. Tegmen small, less than 6 mm long, *c.* 2.5 times longer than wide; costal margin evenly rounded, apical margin somewhat truncate postero-apically; costal margin and ScP+R→ScP+RA more or less parallel, costal space therefore of equal width for entire length; fork of ScP and RA distal to level of primary MP fork; ScP and RA entering antero-apical margin; ScP fairly upright, slightly curved, RA markedly concave, C1a cell broadly ovate; fork of ScP+RA and RP slightly proximal to ½ tegmen length, about midway between basal cell and fork of ScP and RA; RP simple, directed towards apical margin; *ir* short, forwardly inclined; one *rp-mp*, upright, between RP and MP1+2 ; MP1+2 with 2 branches, MP3+4 with 3; *mp-cua* between MP and CuA1; CuA deeply forked, at *c.* ½ tegmen length, well before apex of clavus and primary MP fork, with 2 long parallel branches curved towards posterior margin.

Notes. *Crosbixius* is quite similar to the Russian Permian genus *Surijokocixius* differing only in the costal space of equal width over its entire length rather than expanded basally, the more

basal fork of ScP+RA and RP, and *mp-cua* running between MP and CuA1, rather than MP3+4 and CuA1. It differs from *Scytocixius* in these same three characters, and also in having a branched rather than simple MP3+4, and curved, rather than straight branches of CuA. It differs from *Boreocixius* in the more distal fork of ScP+RA and RP, ScP and RA entering the antero-apical rather than the anterior margin, the broader C1a cell, a simple rather than 3-branched RP, and five rather than seven MP branches; and from *Tricrosbia* in its larger size, differently shaped C1a cell, presence of *ir*, simple RP, 2-branched rather than simple MP1+2, and the deeply forked CuA with curved branches.

Crosbixius carsburgi sp. nov.
(Fig. 2)

Material examined. Holotype tegmen QMF60133, Mount Crosby Formation, Fossil Insect Locality B, collected by Allan Carsburg. Paratype tegmen QMF6978a/b, same locality. Late Triassic (Norian).

Description. Tegmen 5.7 mm long, 2.4 mm wide (both specimens); clavus not preserved; typical fulgoroid post-nodal peripheral membrane clearly developed; base of costal space, base of CuA1 cell, around most veins, and two indistinct posteriorly convergent fascia on the membrane darkly shaded.

Notes. The specific name honours Allan Carsburg of Brisbane who collected the holotype.

Karesmina gen. nov.

Type species. *Karesmina punicea* sp. nov.

Etymology. The generic name is a combination the given names Karen and Jasmine, the spouse and daughter of the collector Allan Carsburg, and is feminine.

Diagnosis. Tegmen larger, *c.* 9 mm long, *c.* 2.5 times longer than wide; apical margin somewhat truncate antero-apically; costal margin and ScP+R→ScP+RA apparently more or less parallel, base of costal space not preserved; fork of ScP and RA at about same level as primary MP fork; ScP and RA entering antero-apical margin; ScP forwardly inclined, fairly straight, RA slightly concave, directed apically, C1a cell broadly triangular; fork of ScP+RA and RP slightly proximal to ½ tegmen length, about midway between basal cell and fork of ScP and RA; RP apparently with 2 branches, directed towards apical margin; *ir* long, backwardly inclined; two apparent *rp-mp*, the proximal one strongly backwardly inclined, between RP and MP1+2 which is deflected anteriorly at this point; the apparent distal *rp-mp* very short, between ?RP2 and MP1 which is also deflected anteriorly; MP1+2 with 3 branches, MP3+4 with 2; *mp-cua* between MP3+4 and CuA1; CuA deeply forked, at *c.* ½ tegmen length, well before apex of clavus and primary MP fork, with 2 long branches curved towards posterior margin and convergent apically.

Notes. As evident in Fig. 3, the tegmen of the type species is indistinctly preserved (? and possibly deformed) in the area of MP1+2 and the distal section of RP. The interpretation of the veins and crossveins in this area can therefore only be considered as tentative. The backwardly inclined vein between RP and MP1+2 is in the same position as the single *rp-mp* in other surijokjocixiids (for example, *C. carsburgi*, see Fig. 2A), and has therefore been interpreted as this crossvein. *Karesmina* gen. nov. differs from all other known surijokocixiids in its larger size (tegmen length 9 mm, length no more than 6 mm in the others), truncate antero-apical margin, long, backwardly inclined *ir*, and peculiar structure of RP and MP1+2.

Karesmina punicea sp. nov.
(Fig. 3)

Material examined. Holotype tegmen QMF60134a/b, Esk Formation, near 5 Mile Creek on the western shore of Lake Wivenhoe, south-eastern Queensland, collected by Allan Carsburg. Middle Triassic (Anisian).

Description. Tegmen fragment 6.4 mm long (indicating a total length of *c.* 9 mm), 4.2 mm wide; clavus not preserved; typical fulgoroid post-nodal peripheral membrane preserved around antero-apical margin; any colour pattern apparently not preserved (darker areas in Fig. 3 are shadows).

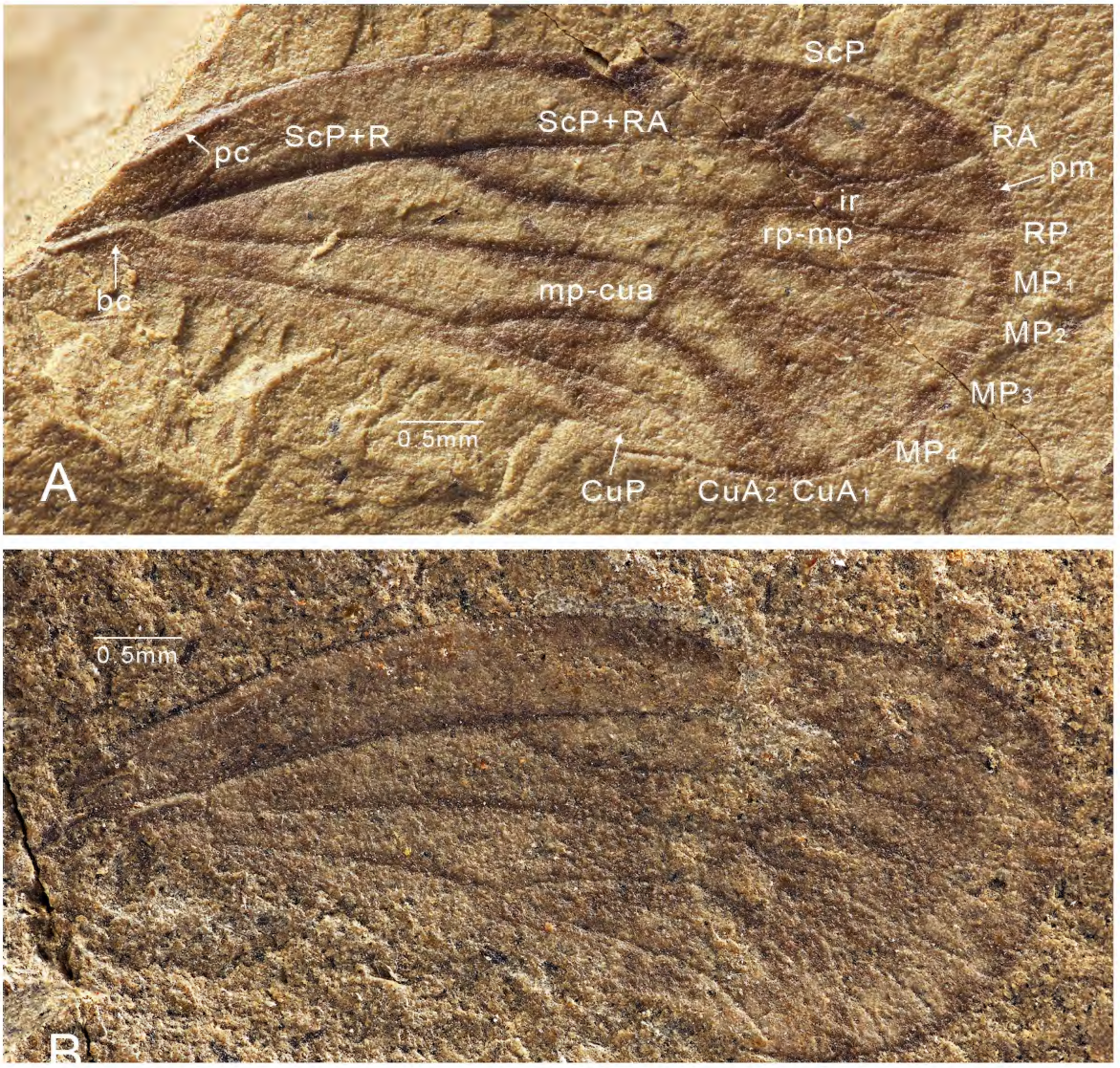

FIG. 2. *Crosbixius carsburgi* gen. *et* sp. nov.; **A**, holotype QMF60133; **B**, paratype QMF6978a (mirrored).

Notes. The specific name is the Latin adjective for pink and refers to the colour of the siltstone in which the type specimen is preserved.

DISCUSSION

While just a few fossil Hemiptera have been found in the Esk Formation, over the last 100+ years hundreds of Hemiptera specimens have been collected from the Mount Crosby Formation and the nearby Late Triassic Blackstone Formation (Lambkin 2019a). The finding of only five specimens of Fulgoromorpha in that time demonstrates their rarity, consistent with Shcherbakov's (2004) observation that the Fulgoromorpha were a minor component of the pre-Jurassic hemipteran fauna. Notwithstanding this rarity, the five specimens represent three species in three genera, suggesting at least some

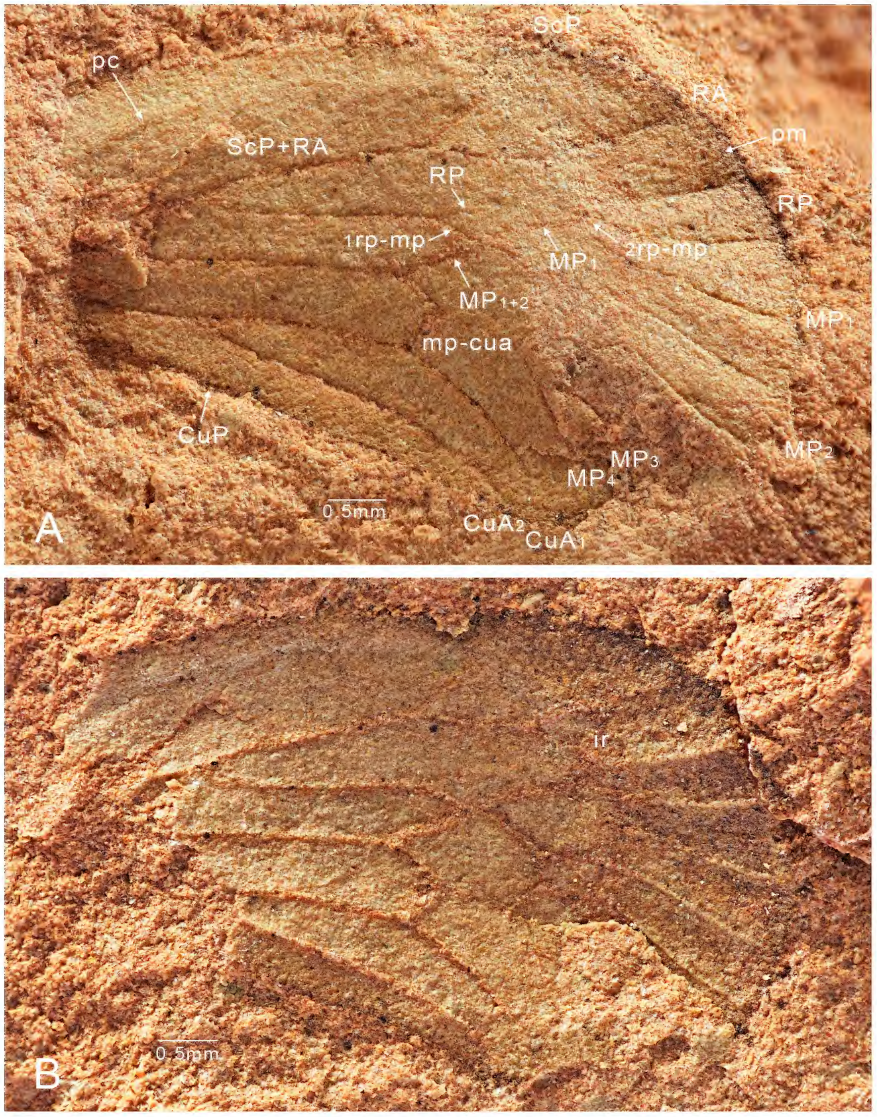

FIG. 3. *Karesmina punicea* gen. et sp. nov. holotype; **A**, QMF60134a (part) (mirrored); **B**, QMF60134b (counterpart), to show ir.

diversity in the fulgoromorph fauna of the Queensland Triassic.

The surijokocixiids were extinct by the end of the Triassic, succeeded in the Jurassic by a much more diverse fulgoromorph fauna, dominated by numerous species of the extinct Fulgoridiidae (Li *et al*. 2011, Szwedo *et al*. 2011). *Tricrosbia* and *Crosbixius* from the Late Triassic (Norian) (~227 – ~208.5 Ma) (International Chronostratigraphic Chart v.2019/5) Mount Crosby Formation were the last of the surijokocixiids. The earliest records of the family, and therefore the oldest fulgoroids, were *Surjokocixius* and *Scytocixius* from the Middle Permian and *Boreocixius* and *Paraprys* from the Late Permian of Russia (Shcherbakov 2008a, 2016). The other Triassic records of the family were from older deposits than

Mount Crosby. The Madygen Formation of Kyrgyzstan (Shcherbakov 2011) has been dated as mid-Triassic (late Ladinian–early Carnian, 237 ± 2 Ma) (Voigt *et al*. 2017), the insect-bearing layer of the Tongchuan Formation of China as Middle Triassic (late Ladinian, 238 – 237 Ma) (Zheng *et al*. 2018), and the Esk Formation (*K. punicea* herein) as Middle Triassic (Anisian, 247.2 – ~242 Ma).

Confirmation of the presence of the Surijokocixiidae in the Mount Crosby Formation adds another family to the Late Triassic (Norian) Hemiptera '*Auchenorrhyncha*' from the long-known and well-collected Mount Crosby and Blackstone formations of the Ipswich Coal Measures. Even though the family composition of the two formations differs, probably due to habitat difference (Lambkin 2019a), the fauna as a whole is a classic transitional insect fauna typical of the Triassic (Shcherbakov 2008b, Zheng *et al*. 2018), with a mix of survivors from the Permian which did not last beyond the Triassic (Dunstaniidae, Scytinopteridae, Surijokocixiidae) or Jurassic (Dysmorphoptilidae), peculiar Triassic endemics (Chiliocyclidae, Mesogereonidae, Ipsviciidae), the newly emerged Hylicellidae which survived until the Cretaceous, and lastly the more modern forms, Archijassidae, the earliest record of the extant Membracoidea (Shcherbakov 2012), and Tettigarctidae, the hairy cicadas, which still exist today (Lambkin 2019b).

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LITERATURE CITED

Allen, R.J. 1961. The Kholo Sub-group of the Ipswich Coal Measures. *Geological Survey of Queensland Publication* **300**: 1–14.

Becker-Migdisova, E. E. 1962. Superorder Rhynchota. Insects with proboscis. Pp 216–317. *In* Rohdendorf, B.B. (ed.) *Fundamentals of Paleontology, vol. 9, Arthropoda, Tracheata, Chelicerata*. (Akademiya Nauk SSSR, Moscow). [In Russian; English translation 1991, Smithsonian Institution Libraries and The National Science Foundation, Washington, DC].

Bourgoin, T. & Szwedo, J. 2008. The 'cixiid-like' fossil planthopper families. *Bulletin of Insectology* 61: 107–108.

Bourgoin, T., Wang, R-R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroiński, A., Yap, S. & Szwedo, J. 2015. From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology* **134**: 63–77 https://doi.org/10.1007/s00435-014-0243-6.

Evans, J.W. 1971. Some Upper Triassic Hemiptera from Mount Crosby, Queensland. *Memoirs of the Queensland Museum* **16**: 145–152.

Hamilton, K.G.A. 1992. Lower Cretaceous Homoptera from the Koonwarra Fossil Bed in Australia, with a new superfamily and synopsis of Mesozoic Homoptera. *Annals of the Entomological Society of America* **85**: 423–430 https://doi.org/10.1093/aesa/85.4.423.

Jell, P.A. 2004. *Fossil insects of Australia. Memoirs of the Queensland Museum* **50**: 1–124.

Jell, P.A. & Lambkin, K.J. 1992. Middle Triassic orthopteroid (Titanoptera) insect from the Esk Formation at Wivenhoe Dam. *Memoirs of the Queensland Museum* **33**: 258.

Lambkin, K.J. 2016. Revision of the Scytinopteridae (Hemiptera: Cicadomorpha: Scytinopteroidea) of the Queensland Triassic. *Zootaxa* **4117**: 580–590 https://doi.org/10.11646/zootaxa.4117.4.9.

Lambkin, K.J. 2019a. Revision of *Mesothymbris* Evans, 1956, from the Late Triassic of Mount Crosby, Queensland (Hemiptera: Cicadomorpha: Hylicelloidea: Hylicellidae). *Zootaxa* **4629**: 389–396 https://doi.org/10.11646/zootaxa.4629.3.6.

Lambkin, K.J. 2019b. *Mesodiphthera* Tillyard, 1919, from the Late Triassic of Queensland, the oldest cicada (Hemiptera: Cicadomorpha: Cicadoidea: Tettigarctidae). *Zootaxa* **4567**: 358–366 https://doi.org/10.11646/zootaxa.4567.2.8.

Li, S., Szwedo, J., Ren, D. & Pang, H. 2011. *Fenghuangor imperator* gen. et sp. nov. of Fulgoridiidae from the Middle Jurassic of Daohugou Biota (Hemiptera:

Fulgoromorpha). *Zootaxa* **3094**: 52–62 https://doi.org/10.11646/zootaxa.3094.1.4.

Martynov, A.V. 1937. Permian fossil insects from Kargala and their relationships. *Trudy Paleontologischeskogo Instituta Akademii Nauk SSSR* **7**: 1–92. [In Russian, with English summary]

Purdy, D.J. 2013. Esk Basin. Pp 387–391. *In* Jell, P. A. (ed.) *Geology of Queensland*. (Geological Survey of Queensland: [Brisbane]).

Purdy, D.J. & Cranfield, L.C. 2013. Ipswich Basin. Pp 391–396. *In* Jell, P.A. (ed.) *Geology of Queensland*. (Geological Survey of Queensland: [Brisbane]).

Raven, R.J., Jell, P.A. & Knezour, R.A. 2015. *Edwa maryae* gen. et sp. nov. in the Norian Blackstone Formation of the Ipswich Basin – the first Triassic spider (Mygalomorphae) from Australia. *Alcheringa* **39**: 259–263 https://doi.org/10.1080/03115518.2015.993300.

Rohdendorf, B.B., Becker-Migdisova, E.E., Martynova, O.M. & Sharov, A.G. 1961. Paleozoic insects of Kuznetsk Basin. *Trudy Paleontologischeskogo Instituta Akademii Nauk SSSR* **85**: 1–705. [In Russian]

Shcherbakov, D. E. 1996. Origin and evolution of the Auchenorrhyncha as shown by the fossil record. Pp 31–45. *In* Schaefer, C.W. (ed.), *Studies on Hemipteran Phylogeny*. (Entomological Society of America, Lanham, Maryland).

Shcherbakov, D.E. 2000. Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permo-Triassic crisis. *Paleontological Journal* **34**: 251–267.

Shcherbakov, D.E. 2004. On Permian and Mesozoic Fulgoroidea. Pp 68–70. *In* Kerzhner, I. M. (ed.) *Third European Hemiptera Congress Abstracts*. (Russian Academy of Sciences: St. Petersburg).

Shcherbakov, D.E. 2008a. On Permian and Triassic insect faunas in relation to biogeography and the Permian–Triassic crisis. *Paleontological Journal* **42**: 15–31.

Shcherbakov, D.E. 2008b. Insect recovery after the Permian/Triassic crisis. *Alavesia* **2**: 125–131 https://doi.org/10.11646/zootaxa.2836.1.1.

Shcherbakov, D.E. 2011. New and little-known families of Hemiptera Cicadomorpha from the Triassic of Central Asia – early analogs of treehoppers and planthoppers. *Zootaxa* **2836**: 1–26.

Shcherbakov, D.E. 2012. More on Mesozoic Membracoidea (Homoptera). *Russian Entomological Journal* **21**: 15–22 https://doi.org/10.15298/rusentj.21.1.02.

Shcherbakov, D.E. 2016. On the taxonomic position of the genus *Parapryg* (Homoptera, Fulgoroidea) and classification of Protorthoptera and related groups. *Paleontological Journal* **50**: 412–413 https://doi.org/10.1134/S0031030116040110.

Szwedo, J. 2018. The unity, diversity and conformity of bugs (Hemiptera) through time. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **107**: 109–128 https://doi.org/10.1017/S175569101700038X.

Szwedo, J., Bourgoin, T. & Lefebvre, F. 2004. *Fossil planthoppers (Hemiptera: Fulgoromorpha) of the world An annotated catalogue with notes on Hemiptera classification*. (Studio 1: Warsaw).

Szwedo, J., Wang, B. & Zhang, H.-C. 2011. An extraordinary Early Jurassic planthopper from Hunan (China) representing a new family Qiyangiricaniidae fam. nov. (Hemiptera: Fulgoromorpha: Fulgoroidea). *Acta Geologica Sinica* **85**: 739–748 https://doi.org/10.1111/j.1755-6724.2011.00479.x.

Tindale, N.B. 1945. Triassic insects of Queensland. 1. *Eoses*, a probable lepidopterous insect from the Triassic beds of Mount Crosby, Queensland. *Proceedings of the Royal Society of Queensland* **56**: 37–46.

Voigt, S., Buchwitz, M., Fischer, J., Kogan, I., Moisan, P., Schneider, J. W., Spindler, F., Brosig, A., Preusse, M., Scholze, F. & Linnemann, U. 2017. Triassic life in an inland lake basin of the warm-temperate biome – the Madygen Lagerstätte (southwest Kyrgyzstan, Central Asia). Pp 65–84. *In* Fraser, N.C. & Sues, H.D. (eds) *Terrestrial conservation Lagerstätten: windows into the evolution of life on land*. (Dunedin Academic Press: Edinburgh).

Zheng, D., Chang, S-C., Wang, H., Fang, Y., Wang, J., Feng, C., Xie, G., Jarzembowski, E. A., Zhang, H. & Wang, B. 2018. Middle-Late Triassic insect radiation revealed by diverse fossils and isotopic ages from China. *Science Advances* **4**(9): 1–7 https://doi.org/10.1126/sciadv.aat1380.

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On the identity of several Queensland camaenids: a reappraisal of their type specimens, accuracy of type localities and their association with extant populations (Eupulmonata: Camaenidae: *Figuladra*).

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ABSTRACT

Species assigned to *Figuladra* Köhler & Bouchet, 2020 (Camaenidae) described prior to 1900 were originally diagnosed entirely on shell morphology, particularly colour and banding pattern. This historical reliance on such highly variable shell characters, together with type localities that were either very broad or sometimes completely erroneous, have created confusion about the correct application of their names to living populations of many Figuladra species. This is evident in both the 19th century and contemporary scientific literature. Species here investigated comprised *Helix incei* Pfeiffer, 1846; *Helix lessoni* Pfeiffer, 1846; *Helix curtisiana* Pfeiffer, 1864; *Helix* (*Camaena*) *praetermissi* Cox, 1868; *Helix (Camaena) aureedensis* Brazier, 1872; and *Helix* (*Camaena*) *challisi* Cox, 1873. This study resolved these historical inconsistencies through a re-examination of type materials as listed by Smith (1992) and their correlation with original descriptions and illustrations, a re-assessment of associated type localities and a consideration of historical events that may have contributed to past inaccuracies. In some cases, purported type specimens bore no resemblance to original descriptions and illustrations and in some instances type localities were completely erroneous or had subsequently been wrongly designated. As a consequence, a number of names have historically been wrongly applied to populations of snails. We provide a reappraisal of the type materials and reassessment of the accuracy of the type localities for the species under consideration.

❑ *Eupulmonata, Camaenidae, Figuladra, type species, type localities, eastern Queensland.*

Figuladra Köhler & Bouchet, 2020 (type species. *Helix curtisiana* Pfeiffer, 1864) is a genus of large camaenid land snails that is particularly speciose in south-east Queensland and central Mackay coast. The genus was introduced by Iredale (1933) and later synonymised under *Varohadra* Iredale, 1933 by Iredale (1937) without reason. Smith (1992) synonymised the genus under *Sphaerospira* Mörch, 1867 along with a number of other Iredalean genera citing Bishop's (1978) anatomical study of *S. fraseri* Griffith and Pidgeon, 1833 as the reason for this taxonomic decision. However, our investigations show that the Bishop study makes no mention of these genera and their possible synonymy. *Figuladra* was re-

elevated to generic status by Stanisic *et al.* (2010) citing differences in animal colour as a key differentiating feature; a red mantle in *Figuladra* species compared to a black mantle in *Sphaerospira* species. Stanisic (2010) included ten species and three subspecies in *Figuladra*. All the usages of *Figuladra* to this time (2010), were deemed to be *nomina nuda* by Köhler & Bouchet (2020) who re-diagnosed the taxon thus making it an available name.

Considerable confusion has surrounded the identity and origin of species, described prior to 1900, that have traditionally been included in this genus. This resulted from a reliance on a taxonomy based solely on shell colour and banding pattern which are known to vary extensively within species in this group of land snails. The confusion was compounded by the lack of accuracy and errors in assigned type localities. The species concerned are *Helix incei* Pfeiffer, 1846; *Helix lessoni* Pfeiffer, 1846; *Helix curtisiana* Pfeiffer, 1864; *Helix (Camaena) praetermissi* Cox, 1868; *Helix (Camaena) aureedensis* Brazier, 1872; and *Helix (Camaena) challisi* Cox, 1873. Smith (1992) made a number of taxonomic decisions concerning these species, and their synonyms, that were based on 'original descriptions and examination of type material'. In doing so he altered the existing taxonomy of Iredale (1937) to a major extent but without detailed explanation. Smith did not have access to a large and geographically extensive collection of contemporary material with which to compare type specimens and judge the accuracy of their type localities. Instead, he relied on dubious identifications of what was then a relatively small subset of local museum specimens for verification.

The Queensland Museum has a sizeable, well curated collection of described and putative *Figuladra* species accumulated over the last 40 years. The geographic coverage of the collection is extensive and shows species and their associated colour morphs appear to be fairly circumscribed in distribution. This has allowed for a thorough re-assessment of the validity of problematic type specimens and their type localities and the correct association of names with living populations. The results of this study show that the decisions of Smith (1992) regarding these six species were flawed in a number of significant aspects. The study also shows that there are historical issues surrounding the type materials that Smith (1992) should have considered when assessing the veracity of types and their type localities. These uncertainties have had a profound and lasting influence on certain species concepts within *Figuladra* as is evidenced by incorrect identifications having been universally applied in museum collections.

Hence, the primary aim of this study was to ensure the correct association of these six species' names with extant populations through the reappraisal of type materials and type locality data. While this process may be more rightly considered an integral part of a more expansive revision of the genus, the detailed and sometimes painstaking resolution of these complex nomenclatural issues merits particular documentation.

ABBREVIATIONS

General. I, Island; MEQ, Mideastern Queensland; NP, National Park; SEQ, Southeastern Queensland; SF, State Forest.

Museums. AM, Australian Museum, Sydney; HMNT, Hancock Museum, Newcastle on Tyne, University of Newcastle, UK; MCZ, Harvard Museum of Comparative Zoology; NHMUK, British Museum of Natural History; QM, Queensland Museum, Brisbane; SAMA, South Australian Museum, Adelaide; ZMB, Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Germany.

MATERIAL AND METHODS

This study is based on type and putative type specimens held by the AM, HMNT, MCZ, NHMUK, SAMA and ZMB. Those in the AM and NHMUK were personally sighted by the authors while images of other specimens were provided by the relevant institutions. These specimens and images were assessed against their original descriptions, illustrations and

subsequent literature citations. Following this assessment, they were compared with specimens in the QM's large and comprehensive collection of *Figuladra* material.

The generic limits of some of the taxa under consideration in this paper are uncertain, so that when we compare extant populations to described taxa, we have elected to use their original combinations.

BACKGROUND

Species that were described in the nineteenth century and are now included in *Figuladra* Köhler & Bouchet, 2020 have a convoluted history. Early conchologists differed in their opinions as to the identities of these species, and these uncertainties persist to the present day (Reeve 1854; Cox 1868; Pilsbry 1890; Iredale 1937; Smith 1992; Stanisic *et al.* 2010). Many of these early species were collected on voyages of survey ships such as the H.M.S. *Fly* (Jukes 1847) and H.M.S. *Rattlesnake* (Macgillivray 1851) and due to the lack of detailed mapping of the Queensland coast at the time, localities were often listed as 'Australia' or 'Northern Australia'. Port Denison (Bowen) and 'Torres Strait' were often used for locations along the coastline north of Port Curtis (Gladstone). Many of these species, including those dealt with herein, were described from the private collections of Hugh Cuming, George French Angas and William Hargraves. The following account details some of the history surrounding their collections and their deposition in accredited institutions.

In the nineteenth century, Hugh Cuming (1791-1865) was an avid shell collector. Few contributed as much to the material advance of natural history as he did. Cuming's collection was more extensive than that of the British Museum who refused to purchase it when offered in 1846. Subsequently many duplicate specimens from Cuming's collection were sold at auction and some were acquired by other museums such as the ZMB. Finally in 1866, the trustees of the British Museum did purchase the collection, comprising 82,922 shells, for £6000 at the time when John Gray was the Keeper of Zoology. Currently the British Museum houses several unregistered *Figuladra* specimens from Hugh Cuming's collection and there is considerable confusion surrounding some of the Cuming collection material and its provenance (pers. obs.). Dance (1980) cites the possible source of this confusion:

> 'There can be no doubt, however, that Gray's wife Maria did more to reduce the scientific value of the collection than anyone else. Shortly after its arrival in the museum she removed the eighty-three thousand specimens from the drawers lined with sheet wool on which Cuming had kept them and glued them on to wooden tablets, a standard practice then. But in the process she carried them drawer by drawer across an open courtyard and many labels were blown into wrong places and consequently gummed to the wrong tablets' (p. 501).

Hedley (1912) also commented on the British Museum's management of its conchological collection from his visit in that year, expressing shock that the museum exhibited their entire shell collection including types on public display and any conchologist working on the shells did so in a dimly lit hall in full view of the public. The specimens themselves were glued to wooden tablets and if they came loose over time, as the gum became brittle, were likely to be misplaced on their return.

George French Angas (1822-1886) was an English malacologist, painter and author. Angas is particularly well known for his shell collecting in South Australia and amassed an extensive private collection of shells. For some time, he worked in Sydney where he held an exhibition of his watercolours. In 1853, Angas was appointed to a position at the Australian Museum in Sydney, eventually becoming secretary and staying a total of seven years. During this period, he supervised the work of classifying and arranging the first public collection of Australian specimens, especially shells, which would have also given him access to the AM collections and collectors of the time

(Morgan 1966). His publications focus more on marine species and nudibranchs than land snails (for example, Adams & Angas 1864, Angas 1865, Adams & Angas 1865, Angas 1867, 1878). He made a donation of 298 shells to the AM (Bramley *et al.* 2008). Part of his private collection was sold in London in 1869. He presented many marine specimens (about 1500) including types to the Natural History Museum (London, UK), but his land snail collection was bequeathed to the HMNT in his native city of Newcastle on Tyne (Hedley 1913, Poppe & Poppe 1994). While Angas had visited Queensland, according to his journal articles on both marine and land shells, he had only collected as far north as Port Stephens, New South Wales (Iredale 1959).

William Hargraves (1838-1925) was the son of Edward Hargraves renowned for his discovery of gold near Bathurst in 1851. William Hargraves worked in the New South Wales State Government Equity Office but spent most of his spare time amassing a sizeable private shell collection which was sold to the Australian Museum, Sydney in 1877 for £800. In 1901, he became a trustee of the museum, a position he held until his death. Through collecting, purchase, exchange and personal persuasion this passionate conchologist stopped at nothing in pursuit of the next desirable specimen. Hargraves did not collect in northern Queensland and relied on others (e.g. ship captains) to collect for him on their journeys, paying them for their shells. As a result, the localities of some specimens could be considered less than trustworthy. John Stanisic (co-author) personally curated the Australian Museum's land snail collection in the late 1970s, and came to the general conclusion that the Hargraves material was consistently beset with problems concerning the provenance of specimens.

From the above historical accounts, an understanding of how and why confusion over the correct application of names for some species, to living populations may have arisen.

In the following investigation, six species described prior to 1900 were considered to belong to *Figuladra*, the species were treated in chronological order of their descriptions. Species accounts feature a discussion of their history from time of collection to their description and deposition in reputable institutions including subsequent literature citations and illustrations. Every attempt has been made to clearly present evidence supporting the decisions made herein, primarily about type material and type localities. No attempt has been made to resolve the synonymies of taxa in Smith (1992) but major inconsistencies were discussed within the limits of this study.

NOMENCLATURAL MATTERS

Helix incei Pfeiffer, 1846
(Figs 1–6)

Helix incei Pfeiffer, 1846 was described in the *Proceedings of the Zoological Society of London* (Part 13) with a publication date of February, 1846 (Pfeiffer 1846a: 126). This was in the same year and month as Philippi (1846 ('1845')) published his book containing the description of taxa from many authors including Pfeiffer. Philippi and other nineteenth century authors such as Cox (1868) and Pilsbry (1890) attributed authorship of this species to Pfeiffer. Since that time, Iredale (1937), Smith (1992) and Stanisic *et al.* (2010) incorrectly listed Philippi as the author. The authorship is corrected herein.

Pfeiffer's description was based on a shell collected by Lieutenant Ince, RN and purchased by Hugh Cuming. This was explicitly stated in Philippi (1846). No illustration was given by Pfeiffer however, Philippi (1846: pl, 7, Figure 3) illustrated the species in his publication (Fig. 1A).

Pfeiffer's description was translated from the original Latin by Reeve (1854) and depicted the shell as:

> 'umbilicated, depressedly globose, rather solid, striated, white, beneath a light fulvous epidermis, encircled with narrow chestnut bands; spire raised, rather sharp; convex, 7 whorls, the last rather compressed around the umbilicus, which is middling and open; columellar arched; aperture very oblique,

> lunar-oval; lip white, thin, slightly thickened inwardly, right margin a little expanded; basal margin reflected, columellar margin dilated into a triangular lamina which half conceals the umbilicus. Diameter 38 mm, height 28 mm' (p. 113). The locality is given as 'Northern Australia'.

Reeve (1854) stated that there were colour variations in the shell of this species and illustrated two forms, one banded and one darker where much of the shell is covered by a brown suffusion (Fig. 1B). Following comparison with contemporary material collected from the Percy Islands, Reeve's illustrations are considered a true representation of *Helix incei*.

Cox (1868) recognised Pfeiffer as the author of *H. incei* and recorded the species as occurring from Ipswich through to Port Curtis (Gladstone), MEQ. Cox commented that the shell was 'subject to considerable variation' and could vary with locality (1868: 55); understandably so, since this range now includes multiple species previously all recognised as *H. incei*. Cox (1868) illustrated two specimens, one of unknown origin (pl. 5. Figure 5), and another from Wide Bay (pl. 18, Figure 1) showing a dark lip dissimilar to *H. incei* figured in Philippi (1846) and Reeve (1854). Both images were referenced by Hedley (1888) under his listing of *H. incei.* The former Cox image is an indeterminate species and does not fit the original description of *H. incei*. The latter image was also recognised as an error by Tryon (1888:134) who correctly stated that this image was of the species *Helix (Hadra) bayensis* Brazier, 1875 now recognised as *Figuladra bayensis* from the Wide Bay area, SEQ.

Pilsbry (1890) portrayed *H. incei* as a light buff shell with spiral bands of chestnut with one wider band just under the suture. Pilsbry stated (1890), '*Helix incei* is found in every part of Queensland in the open forest country' (p. 166). This would suggest an early confusion with *Figuladra mattea* (Iredale, 1933) which is a spirally banded, widespread species living in open woodland, unlike *H. incei* which is found in vine thicket.

Iredale (1937) assigned *H. incei* to *Varohadra* Iredale, 1933. The type locality cited by Pfeiffer (1946a) was 'Northern Australia' and Iredale (1933), knowing that *H. incei* was collected by Lieutenant Ince on the voyage of the H.M.S. *Fly*, surmised the type locality to be Port Denison (Bowen). There is however, no record of this shell from the Port Denison in the log of the *Fly*. Later, Iredale (1937) observed that although this name had also been used for specimens found around Port Curtis, Macgillivray on the voyage of H.M.S. *Rattlesnake* had logged a specimen of *H. incei* collected from the largest of the Percy Islands (3 December, 1847). As a result, Iredale (1937) correctly restricted the type locality for *H. incei* to the Percy Islands noting:

> 'Though this specific name has been used for shells from Port Curtis, it had been collected by Ince, who did not visit that locality. I noted that Port Denison was a better locality, but Forbes, from the personal knowledge of Macgillivray, recorded "Percy Isles, Keppel Is., Port Molle". The figure shows an elevated shell, and specimens from the Keppel Isles and Port Molle are both depressed, so "Percy Isles" is here designated as type locality of *incei*' (Iredale 1937: 33).

Smith (1992) reclassified *Varohadra incei* as *Sphaerospira incei* but split the species into three subspecies: *viz. S. incei incei* (Pfeiffer, 1846), *S. incei lessoni* (Pfeiffer, 1846) and *S. incei curtisiana* (Pfeiffer, 1864). Smith's decision, as stated in the catalogue, was based on 'original descriptions and the examination of types' (p. 156). No other details were given. The distribution of *S. incei incei* was stated as ranging from Gympie to Mackay, Qld, with a list of questionable synonyms which Smith considered were mere colour morphs whose status was yet to be resolved.

More recently, Stanisic *et al.* (2010) followed the classification of Smith (1992) but reassigned the three subspecies to *Figuladra*. The accompanying illustrations of *Figuladra incei incei* (Pfeiffer, 1846) comprise a pale shell from Shoalwater Bay, MEQ, and a banded shell from the Yeppoon area, MEQ (Fig. 1C). However,

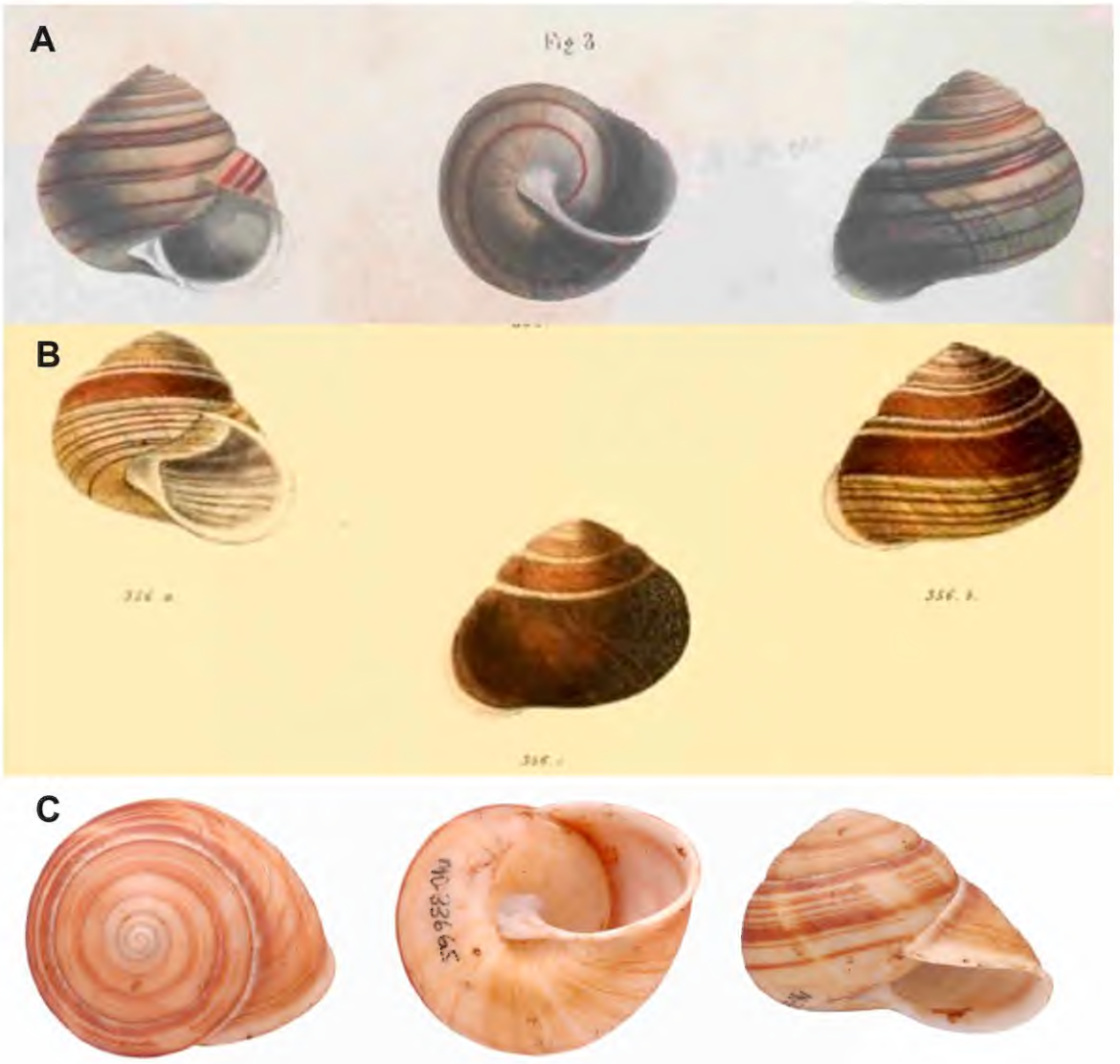

FIG. 1. **A**, *Helix incei* Pfeiffer, 1846: pl. 7, figure 3. **B**, *Helix incei* as illustrated by Reeve (1854) showing two forms. **C**, *Figuladra incei incei* illustrated erroneously in Stanisic *et al.* (2010), QMMO33665, Shoalwater Bay, MEQ). Image C: from Stanisic *et al.* (2010).

investigations into the true type locality of *Helix incei* (below) prove that the images from these localities are misidentifications and instead are images of an unidentified population from the Shoalwater Bay area resembling *Helix (Camaena) praetermissi* Cox, 1868 (uppermost image) and a banded morph of *Helix (Camaena) aureedensis* Brazier, 1872 from Yeppoon (lower image) respectively (see below under these species).

Smith (1992) deferred to Iredale's (1937) designation of the Percy Isles as the type locality of *Helix incei* but cited a 'doubtful holotype' from the South Australian Museum (Fig. 2A). The specimen (SAMAD14513) is labelled as coming from Brisbane, SEQ with the rider '= Percy Is,?'

FIG. 2. Mis-identified species of *Figuladra mattea* (Iredale,1933). **A**, labelled as 'probable holotype', *Helix incei*, SAMA D14513, Brisbane, SEQ. **B**, labelled as a syntype, *Helix incei*, MCZ315889, Northern Australia, ex J.G. Anthony. Scale bars: 10 mm. Images: A, SAMA; B, MCZ.

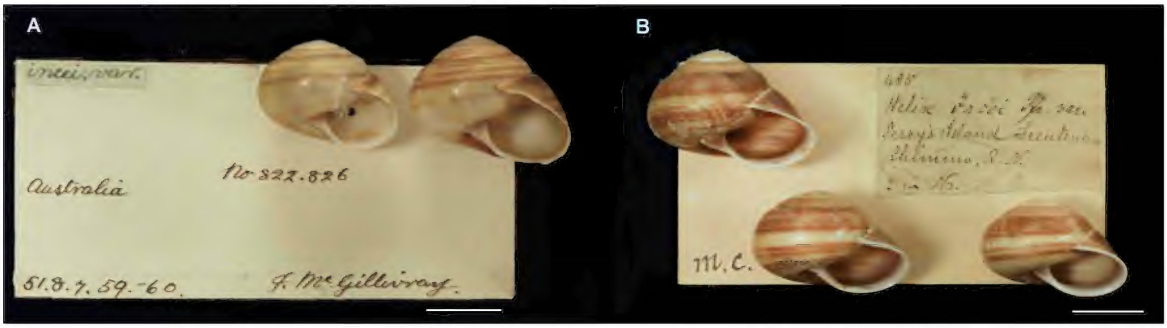

FIG. 3. **A**, NHMUK51.8.7.59 and NHMUK51.8.7.59, specimens collected on the voyage of the H.M.S *Rattlesnake* in 1847. **B**, three unregistered specimens from the Percy Islands, MEQ collected by Lieutenant Commander Chimmo R.N., from the Cuming collection (probably in Pfeiffer's handwriting). Scale bars: 10 mm. Images: JS courtesy of NHMUK.

which appears to be a recent addition to the data label. This shell does not match the original description of the species nor Reeve's images of the shell. Furthermore, no species resembling the SAMA specimen have been found on the Percy Islands. Following examination of the image of the SAMA specimen, we conclude that it is *Figuladra mattea* (Iredale, 1933) which occurs in the Brisbane area.

The MCZ also claims to have a syntype of *H. incei* (MCZ315889) assumed to have been collected by Commander Ince and donated by American collector, John G. Anthony ex. Hugh Cuming collection. The specimen is recorded as coming from 'Northern Australia' (Fig. 2B). This specimen is very similar to the SAMA specimen and we also consider it to be *Figuladra mattea.*

Absent from the NMHUK is designated type material of *H. incei* (J. Ablett, pers. com.) remarkable, considering the material collected on the Fly expedition should have been lodged at that institution. Personal inspection revealed however, that a number of specimen lots labelled *H. incei* exist in the general collection. These comprise of two specimens collected by John Macgillivray on the Voyage of the Rattlesnake in 1847 (from Northern Australia) and three

FIG. 4. *Helix incei* Pfeiffer, 1846. NHMUK20200001 from the Cuming collection collected by Lieutenant Ince in the Percy Islands, MEQ. Scale bar: 10 mm. Image: NHMUK.

specimens from the Percy Islands collected by Lieutenant Commander Chimmo RN (Figs 3A, B). Chimmo was captain of the steamer H.M.S *Torch,* that sailed to the Percy Islands to retrieve the bodies of Frederick Strange and his companions following their murder during the voyage of the ketch *Vision* (Moreton Bay Courier, Chimmo RN 1855).

The most noteworthy of the NHMUK specimens, in the general collection, is one labelled 'collected by Commander Ince' on the Voyage of the H.M.S. *Fly*. In February, 1843, when the H.M.S. *Fly* was anchored at 'Port Denison' and the coastline was explored as far south as Broadsound and Shoalwater Bay, Ince was sent to the Percy Islands to find water (Jukes 1847: 32). The provenance of this specimen would suggest that this was one of the original shells from Cuming's collection used by Pfeiffer for his description. Given the associated locality of 'Northern Australia' (cited by Pfeiffer), we consider this specimen (recently registered as NHMUK20200001) to be part of the original type series that Pfeiffer studied and, in the absence of any other type material, it should be designated as the lectotype of *H. incei* as per the ICZN (2012) (see Fig. 4).

There are three additional unregistered lots purportedly of *H. incei* from the collection of Hugh Cuming in the NHMUK (Fig. 5). However, personal inspection of these specimens revealed they belong to three possibly unrelated species.

An inspection of the Percy Islands camaenids in the collections of both QM and AM reveal specimens matching Pfeiffer's (1846a) original description and both forms depicted in

FIG. 5. NHMUK specimens identified as *Helix incei* Pfeiffer, 1846 but not this species. **A**, *Bentosites coxi* (Crosse, 1866) from the Whitsunday area, MEQ; **B**, *Figuladra mattea* (Iredale, 1933); **C**, *Helix* (*Camaena*) *aureedensis* Brazier, 1872. Scale bars: 10 mm. Images: J. Ablett, NHMUK.

FIG. 6. *Figuladra incei incei* (Pfeiffer, 1846). **A**, AMSC132840, South Percy I, MEQ. **B**, QMMO19146, Pine Islet, MEQ. Scale bars: 10 mm. Image A: JS courtesy of QM; Image B: John Stanisic.

Reeve's (1854) illustration with the dark, broad subsutural band and a brown suffusion on the latter part of the body whorl (Figs 6A, B). Specimens collected more recently on South Percy I by Catherine Radclyffe (March, 2020) also correspond to the illustrations provided by Philippi (1846) and Reeve (1854). Furthermore, the QM collections illustrate that similar shell colour morphs occur only in the Percy Island snails and may be indicative of an isolated population or restricted species. The only other camaenid occurring on the islands appears to be the widespread *Xanthomelon pachystylum* (Pfeiffer, 1845).

We consider therefore, that the name *Helix incei* Pfeiffer, 1846 should apply only to the populations on the Percy Islands, until such time as additional research proves otherwise.

***Helix lessoni* Pfeiffer, 1846**
(Figs 7–9)

Pfeiffer (1846b: 71) described *Helix lessoni* as:

> 'a shell with covered umbilicus, globular, minutely striated, solid, chestnut, paler base; spire turbinate, obtuse, six whorls, slightly convex, last inflated, deflected in front; aperture lunar-rounded, lilac within; lip expanded throughout, white, columellar margin broadly dilated, thickened, white, partly covering umbilicus. D = 35 mm, H = 25 mm. Pfeiffer (1846b) provided 'Australia' as the type locality for *Helix lessoni.*'

Reeve (1854: species 754) translated Pfeiffer's description from Latin but omitted the detail of the paler base (Fig. 7A). This single omission has ramifications for the ultimate identity of this species as the taxonomic decisions of Cox (1868) and Iredale (1937) were based on an understanding that the species had a solid chestnut shell with a dark base. In contrast, Smith (1992) cited purported syntypes of the species that comprised a series of yellowish shells (see below).

Cox (1868) described and illustrated a blackish-chestnut 'variable shell usually to be recognised at once among its allies by its comparatively small size' (p. 55). However, in his description he stated, 'apex sometimes spirally lined, base convex frequently showing traces of spiral lines and bands especially within the mouth'. His description of *H. lessoni* does not conform entirely with that of Pfeiffer's (1846b) original description in that the banding element in the spire and umbilicus were additions. These additional characters suggest that Cox's shell was most likely an undescribed species found in the Mt Larcom area which is west of Port Curtis. Cox also named the type locality of *H. lessoni* as Port Curtis, stating that this species could be found from Miriam Vale to Port Curtis. This is consistent with the known range of the species.

Pilsbry (1890) agreed with Cox's description also referring to 'the spire yellowish or lighter brown, often showing spiral brown lines' and the spiral bandings inside the base. The shells he described and figured (pl. 33, figs 61-63) (Fig. 7B) agree with what was universally recognised as *H. lessoni* at the time. Pilsbry commented that Pfeiffer's (1846b) description indicated a smaller form, differing somewhat in colouration and Pilsbry (1890) figured what he said were Pfeiffer's representations on pl. 35, figs 14, 15 (Fig. 7C). Pilsbry also nominated Port Curtis as the type locality for *Helix lessoni.*

Hedley and Musson (1892) considered the species to be a variant *viz. H. incei var. lessoni* and indicated that he (Musson) had also collected shells of *H. lessoni* on Facing I, Boyne I and in Rockhampton. Hedley and Musson (1892) however, did not mention other species considered to extend the Port Curtis area (e.g. *Helix curtisiana* Pfeiffer, 1864).

Iredale (1933) realised that *H. incei, H. lessoni* and *H. curtisiana* were often mistaken for one another. He also commented that *H. lessoni* and *H. curtisiana* could possibly be the same species, with *H. lessoni* being the 'anterior' name (senior synonym). Iredale recognised that *H. lessoni* appeared to be the common shell at Port Curtis and also occurred on Boyne Island. However, he included no further discussion or conclusions. Iredale noted similar confusion with *Helix (Camaena) aureedensis* Brazier, 1872,

stating that 'the mainland shell recently known as '*aureedensis*' is a relative of '*lessoni*' but is more elevated, darker coloured, with a broad, pale, circum-umbilical patch' (Iredale, 1933, p. 45). Subsequently, Iredale (1933) assigned *Helix lessoni* to a new genus *Varohadra*. Iredale (1937) decided that *H. lessoni* may have come from the islands north of Port Curtis and restricted the type locality of *Helix lessoni* to the Percy Islands assuming that the shell might have been collected on the Voyage of the H.M.S. *Fly*.

Smith (1992) reclassified *Varohadra lessoni* as *Sphaerospira incei lessoni* (Pfeiffer, 1846). Smith's decision as stated in the catalogue was based on 'original descriptions and the examination of types'. No other details were given. The distribution of *S. incei lessoni* was given as 'Queensland' with two questionable synonyms, discussed below. Smith also deferred to Iredale's (1937) incorrect assertion that the Percy Isles were the type locality of this taxon.

Stanisic *et al.* (2010) followed Smith (1992) in regarding *H. lessoni* as a subspecies of *H. incei* which they placed in *Figuladra*. The accompanying illustration of *Figuladra incei lessoni* featured a shell from Yeppoon, MEQ, with a dark spire and pale yellow base. While this specimen was then considered to represent *H. lessoni* in QM and AM collections, investigations show that it is in fact the dark morph of *Helix (Camaena) aureedensis* Brazier, 1872 from the greater Yeppoon area, MEQ (Fig. 7D) (see discussion under that species below).

A holotype of *H. lessoni* was not nominated by Pfeiffer although Philippi mentions the repository as being the British Museum. Smith (1992) cited specimens (NHMUK1844.12.6.70-71, NHMUK1859.3.11.3) as syntypes but wrongly indicated four specimens when the registration details indicate that only three are represented. These three specimens were borrowed in the early 1990s by JS for an intended taxonomic study of large Queensland camaenids. Consequently, one of the putative syntypes was labelled as the lectotype (NHMUK1844.12.6.70) and the remaining two as paralectotypes (NHMUK1844.12.6.71, NHMUK1859.3.11.30) of *H. lessoni*, prior to the material being returned

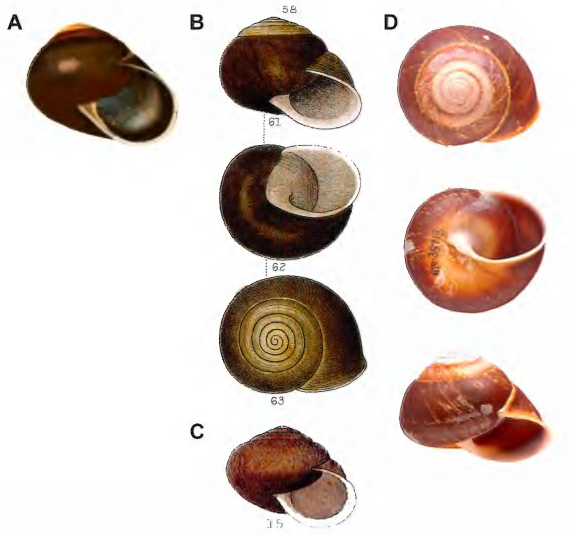

FIG. 7. *Helix lessoni* Pfeiffer, 1846. **A**, as illustrated by Reeve (1854). **B,** as illustrated in Pilsbry (1890 pl. 33, figs 61-63) showing fine banding on the protoconch and in the umbilicus. **C,** as represented by Pfeiffer (1846) but illustrated by Pilsbry (1890, pl. 35, figs 13-15). **D,** as erroneously illustrated in Stanisic *et al.* (2010), QMMO35713, Yeppoon, MEQ. Image D: from Stanisic *et al.* (2010).

to NHMUK. The subsequent designations by JS, were based solely on Smith's citation of specimens as syntypes of *H. lessoni*. In hindsight, reference to Pfeiffer's original description would have flagged an error in identification of these specimens as *H. lessoni*. The three supposed syntypes all have a yellowish to light brown spire with a yellowish base unlike Pfeiffer's description of a blackish, chestnut-coloured shell with a paler base (Figs 8A–C).

A note by Fred Naggs (scientific associate of the NHMUK) in December 1985, is attached to this series of shells and states, 'there are apparently 2 lots mixed here but both could have been seen by Pfeiffer, originally 5 specimens'. This note might have strengthened Smith's belief that these specimens were part of the original type series but the contents of the note also introduce an element of doubt as to their status. Given the shell specimens lack records on type status, provenance (how they came to the

FIG. 8. Putative syntype specimens of *Helix lessoni* Pfeiffer, 1846 erroneously cited by Smith (1992). **A,** lectotype NHMUK1844.12.6.70. (*H. aureedensis*). **B**, paralectotype, NHMUK1844.12.6.71. **C,** paralectotype, NHMUK1859.3.11.30. Scale bars: 10 mm. Images: J. Ablett, NHMUK.

collection) nor match the original descriptions, we do not consider them part of the original type series. These shells, labelled from 'Australia', were from the collection of the Earl of Derby, the then President of the Linnaean Society (1828-1833) a noted naturalist and collector (Figs 8B, C). Accompanying labels indicate that some of these shells were acquired from John Macgillivray whose extensive log of travels did not mention finding *H. lessoni* in his journal listing of species collected on his expeditions. A thorough inspection of the NHMUK collections, that were cited as the repository of Pfeiffer's original specimens (Pfeiffer, 1846b), did not locate any putative type material of *H. lessoni*. This was in spite of the fact that Reeve's (1854) reference to *H. lessoni* was based on a specimen from the Cuming collection that was acquired by the NHMUK.

Pfeiffer's personal collection was housed in the Stettin Museum, Poland, which was destroyed in World War II. However, prior to the war, specimens had been exchanged with the ZMB. The ZMB has two shells from the type series of *H. lessoni* (ZMB Moll. 65914) originating from Pfeiffer's own collection (Fig. 9). These specimens are labelled cotypes and align with Pfeiffer's original description and Reeve's photograph of a dark shell with a white lip, dark aperture and a paler base. Furthermore, a close inspection shows evidence of the apical banding mentioned by Cox (1868) and Pilsbry (1890). As these ZMB specimens are considered part of the type series, we consider these specimens to be part of the original type series Pfeiffer studied, and in the absence of any other type material, these specimens should be designated as the lectotype and paralectotype of *H. lessoni* as per the ICZN (2012) .

QM and AM collections do not contain any shells from the Percy Islands resembling *H. lessoni.* These islands are the type locality of *Helix incei* which is known to have dark colour morphs. However, these dark morphs differ from *H. lessoni* in having bands, including a broad subsutural band, visible below a darker

suffusion. We consider that Iredale's (1933) insinuation of Port Curtis as a possible type locality of *H. lessoni* (also cited by Cox and Pilsbry) is correct and that this name should be applied to extant populations in the Port Curtis area.

Helix curtisiana Pfeiffer, 1864
(Figs 10–12)

Pfeiffer (1864: 528) described *H. curtisiana* from the George French Angas collection without illustration. He described (translated from the original Latin):

> 'a conoidly-semi-globose shell with a narrow umbilicus, striated, and a solid chestnut colour; the spire with a conoidly-convex lighter apex and a suture with a white thread; 6 whorls, slowly increasing with the last large, convex, somewhat angular above the middle. The shell is flattish at the base, descending in front with an aperture nearly diagonal and roundly-lunate with the peristome scarcely thickened. The narrowly expanded columellar margin is triangularly dilated above. Narrow umbilicus. Diameter = 29 mm, Height = 17 mm. The type locality was cited as Port Curtis.'

In his monograph on Australian land snails, Cox (1868: pl. 20, figs. 9 and 9a) illustrated *H. curtisiana* from a painting of the type by George French Angas (Iredale 1937:32) (see Fig. 10A). When Cox was preparing this monograph, he asked Angas to examine some species in the British Museum. There are no corresponding *H. curtisiana* specimens from the Angas collection in the collections of the British Museum. NHMUK's camaenid collection contains only eight lots of *Helix curtisiana* specimens and none from Angas's collection. The only Angas specimen of this species resides in the HMNT where Angas's collection of Australian land snails, including many types, was donated after his death.

Angas prepared coloured paintings which Cox included in two additional plates. This explains an anomaly, as Cox stated on the title page 'eighteen plates', whereas there are

FIG. 9. *Helix lessoni* from Pfeiffer's collection (ZMB Moll. 65914). Note the striated, chestnut shell with dark umbilical patch and dark aperture. Scale bars: 10 mm. Images: ZMB.

twenty in the monograph (Iredale 1959). It can be surmised that Angas painted the shell depicted on plate 20 from one in his personal collection as indicated by Pfeiffer (1864).

Pilsbry (1890) synonymised *Helix bala* Brazier, 1878 (a similar looking shell from Magnetic Island, north Queensland) with *Helix curtisiana,* though we consider this to be an error. Pilsbry's illustrations of the latter (pl. 47, figs 90-91) resembled the species as it was shown by Cox (1868).

Iredale (1933: 45) deemed it likely that *Helix curtisiana* and *H. lessoni* were identical, with *H. curtisiana* being the junior synonym. However, he did not formally synonymise the two species

FIG. 10. *Helix curtisiana* Pfeiffer, 1864. **A**, as illustrated by Cox (1868) from a drawing by Angas. **B**, as illustrated by Stanisic *et al.* (2010), QMMO72398, Tannum Sands, SEQ.

FIG. 11. *Varohadra curtisiana exedra* Iredale, 1937. AMSC100672, holotype, Boyne I., SEQ. Scale bars: 10 mm. Image: AM.

at that time, nor did he in his faunal checklist (Iredale 1937).

Iredale (1933) reclassified *Helix curtisiana* as *Varohadra curtisiana* and at the same time, described a subspecies *Varohadra curtisiana exedra* with type locality of Boyne Island, Port Curtis (Fig. 11). The holotype of *V. curtisiana exedra* in the AM (AMSC100672) does have an indistinct supra-peripheral band and paler base similar to that of *H. curtisiana* figured by Cox (1868) and Pilsbry (1890). This subspecies was considered to be a synonym of *H. curtisiana* by Smith (1992).

Smith (1992) reclassified *Varohadra curtisiana* as *Sphaerospira incei curtisiana* (Pfeiffer, 1864). Smith's decision as stated in the catalogue was based on 'original descriptions and the examination of types'. No other details were given. He gave the distribution of *S. incei curtisiana*

as Queensland and listed three synonyms, including Iredale's (1933) *V. curtisiana exedra*.

Stanisic *et al.* (2010) followed the subspecific classification of Smith (1992) but reassigned the subspecies to *Figuladra*. The accompanying illustration of *Figuladra incei curtisiana* featured a shell from the type locality area of Port Curtis (Fig. 10B).

Smith (1992) cited a 'probable holotype' of *H. curtisiana* from the HMNT but with no registration number. This specimen, now labelled by this museum as 'NEWHM:HANM.1.3531', is a worn specimen with a brown to light brown shell and vague brown spiral bands and is purportedly from Port Curtis, coming from the Angas collection (Fig. 12A). More than 100 years ago, Hedley (1913) reported that he had visited the HMNT and examined the types of Australian land snails from Angas' collection residing there and itemised the 40 specimens in a list, all of which were marked 'type'. *Helix curtisiana* was one such type listed (Hedley 1913: 260).

The HMNT specimen matches images in Cox (1868) and Pilsbry (1890), though has a lighter umbilicus that Pfeiffer did not mention in his description, referring instead to a solid chestnut shell. This specimen also agrees with specimens of *H. curtisiana* from Boyne Island in the QM collections (Fig. 12 B).

While the type locality of *H. curtisiana* was cited as Port Curtis, additional details on a more specific collection site are not available. Macgillivray (1851), during the voyage of the H.M.S. *Rattlesnake*, described Port Curtis as a 10-mile strip of land between Facing Island and Curtis Island to the north. Despite a three-week survey during this section of the voyage in 1847, this land snail was not found by Macgillivray. This area is now the site of Gladstone and much of the original habitat has been destroyed. Round Hill is also a site mentioned in early collections, but Gladstone city now subsumes this hill. Remnant vine thickets on Boyne Island and nearby Tannum Sands are one of the few areas remaining where this species is still present. There are specimens in the QM and AM that we consider to be

FIG. 12. **A,** Confirmed holotype of *Helix curtisiana* Pfeiffer, 1864, Hancock Museum, NEWHM:HANM.1.3531. **B,** *Figuladra curtisiana* (Pfeiffer, 1864), QMMO78028, Boyne I, SEQ. Scale bars: 10 mm. Image A: https://gbmolluscatypes.ac.uk/specimens/534, Creative Commons Attribution-Non Commercial-Share Alike 4.0 International License; Image B: JS courtesy of QM.

H. curtisiana, recorded from both Facing and Curtis Islands and on Rodd's Peninsula where the species is found with and without banding on the early whorls. Iredale (1937) nominated Mt Larcom as the type locality of *H. curtisiana.* This designation is considered an error as this location is home to Camaenid SQ19, a putative sister species which has a dark morph resembling *H. curtisiana.* In order to avoid further confusion, a restricted type locality of Boyne Island, SEQ, where shells closely matching the one in Angas' collection can be found, is herein proposed.

The single HMNT specimen is herein confirmed as the holotype of *Helix curtisiana* as evidence exists that this shell is from the Angas collection and is the one that was described by Pfeiffer (1864).

The shells of *H. curtisiana* and *H. lessoni* share similar descriptions and historically, both have been associated with the Port Curtis locality by early conchologists. Collections of shells at both the QM and AM illustrate that it is highly unlikely that there are two species in the Port Curtis area. This raises the possibility that *Helix lessoni* and *Helix curtisiana* are synonymous. This issue will be resolved in a forthcoming revision of the *Figuladra* clade.

FIG. 13. Cox's (1868: pl. 20, Figure 13) illustration of *Helix (Camaena) praetermissi.*

***Helix (Camaena) praetermissi* Cox, 1868**
(Figs 13, 14)

Cox (1868) introduced *Helix (Camaena) praetermissi* in the additional appendices to his monograph (Cox 1868:111). He described the shell as:

> 'deeply, openly and rather narrowly umbilicated, globose, solid, closely and finely striated, glossy, uniformly of a pale brownish-yellowish colour, obscurely banded with fine pale chestnut lines; spire obtusely conical; convex, 7 whorls, the last inflated and deflected in front; base rounded; aperture roundly-lunate, pure white within; peristome white, thickened and slightly reflected, margins approximating, joined by a thin callus, columellar margin shortly dilated at the base ½ covering the umbilicus. Diameter 1.13- 1.2 inches; height 1.08 inch' (Fig. 13).

Cox noted that this specimen was collected during the voyage of the H.M.S *Rattlesnake* by Macgillivray who was engaged to help prepare his monograph (Calaby 1967). The type locality of this species was given as Cape Direction in northern Queensland which was considered an error by Hedley (1888). The H.M.S. *Rattlesnake* did anchor at Cape Direction in August 1847, but also anchored at Great Keppel I in December of the same year. Macgillivray, who is recorded as being the first European to set foot on the Keppel islands, landing near Leeke's Creek, Great Keppel I., detailed the visit in his log (Macgillivray 1851: 64). Cox's description (1868: 111) referred to the 'late Mr Macgillivray' who had died of a heart attack during his employment with Cox. At the time, Cox considered the species closely allied to *H. incei* and *H. curtisiana,* though unique.

Iredale (1937) reassigned *H. praetermissi* to *Varohadra* but he also questioned the type locality as doubtful. Given MacGillivray's death during his work with Cox, it is possible that a locality error could have been made by Cox during this period.

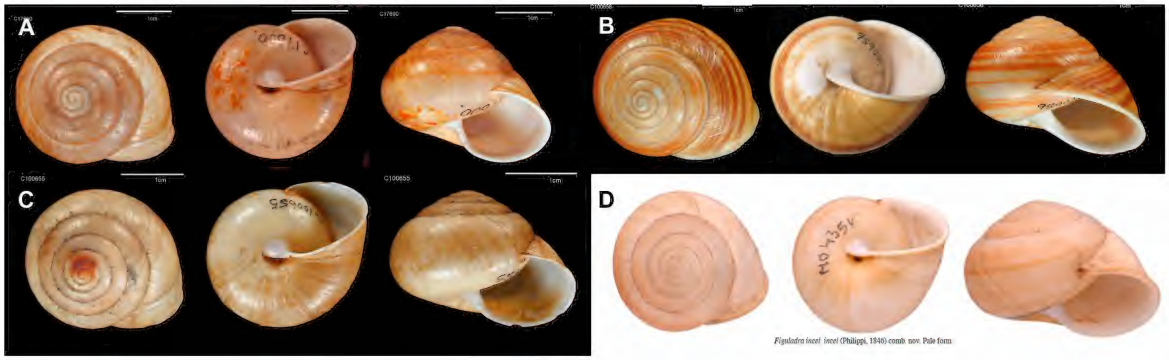

FIG. 14. **A,** *Helix (Camaena) praetermissi* Cox, 1868, AMSC17600, holotype. **B,** *Varohadra keppelensis* Iredale, 1937, AMSC100656, holotype. **C,** *Varohadra keppelensis degener* Iredale, 1937, AMSC100672, holotype. **D,** *Varohadra keppelensis* as erroneously illustrated as *Figuladra incei incei* in Stanisic *et al.* (2010: Species 753, QMMO4358, Keppel Islands, MEQ). Scale bars: 10 mm. Images: A-C, AM; D from Stanisic *et al.* (2010).

Iredale (1937) described *Varohadra keppelensis* Iredale, 1937 from the Keppel Islands, with a brief description separating it from *H. incei* and *H. challisi*. Iredale noted that shells of *V. keppelensis* were large and solid on North Keppel I, and smaller, thinner and less elevated on South Keppel I (Great Keppel I) and some had more 'lines' (bands) than others. He described the snail from South Keppel I as a subspecies, *V. keppelensis degener* Iredale, 1937.

Smith (1992) synonymised *H. praetermissi, V. keppelensis* and *V. keppelensis degener* under *Sphaerospira incei incei* (Pfeiffer, 1846) with the comment that this was done after examination of the types but with the status of the morphs remaining unresolved. Our examination of these types and comparison with Cox's (1868) description and illustration of *H. praetermissi* indicates that it is a senior synonym of *V. keppelensis* and *V. keppelensis degener* (Figs 14 A-C) but is not conspecific with *H. incei* which is found in the Percy Island group. Stanisic *et al.* (2010) followed Smith's classification.

The holotype of *Helix (Camaena) praetermissi* (AMSC17600) is in the collections of the AM. Based on comparative material in the AM and QM , we consider that *Helix (Camaena) praetermissi* should only apply to populations on the Keppel Islands pending the outcome of future studies. In light of the fact that Macgillivray only recorded a shell of this description from Great Keppel Island, we consider that these islands represent a more suitable type locality.

Helix (Camaena) aureedensis Brazier, 1872

(Figs 15, 16)

Brazier (1872) described *Helix (Camaena) aureedensis* from the Hargraves collection as coming from Aureed Island in the Torres Strait. The shell was depicted as:

> 'umbilicated, depressedly globose, rather solid, very finely obliquely striated, and, under the lens finely granulated, dark chestnut; suture ornamented with a fine white thread, and also a broad dirty white undefined zone round the umbilicus; spire broadly conoid, obtuse; whorls 6 to 61/2, convex, the five upper whorls of a reddish chestnut, the last increasing in size, rounded and deflected in front; base convex; aperture diagonally ovately lunate, brownish white within; peristome straight, ivory-white, slightly thickened and reflected; margins approximating, right margin expanded, columellar margin arcuate and reflexed, concealing nearly half of the umbilicus, which is deep' (p. 640).

Personal inspection confirms the holotype shell (AMSC17604) fits with Brazier's description (Fig. 15).

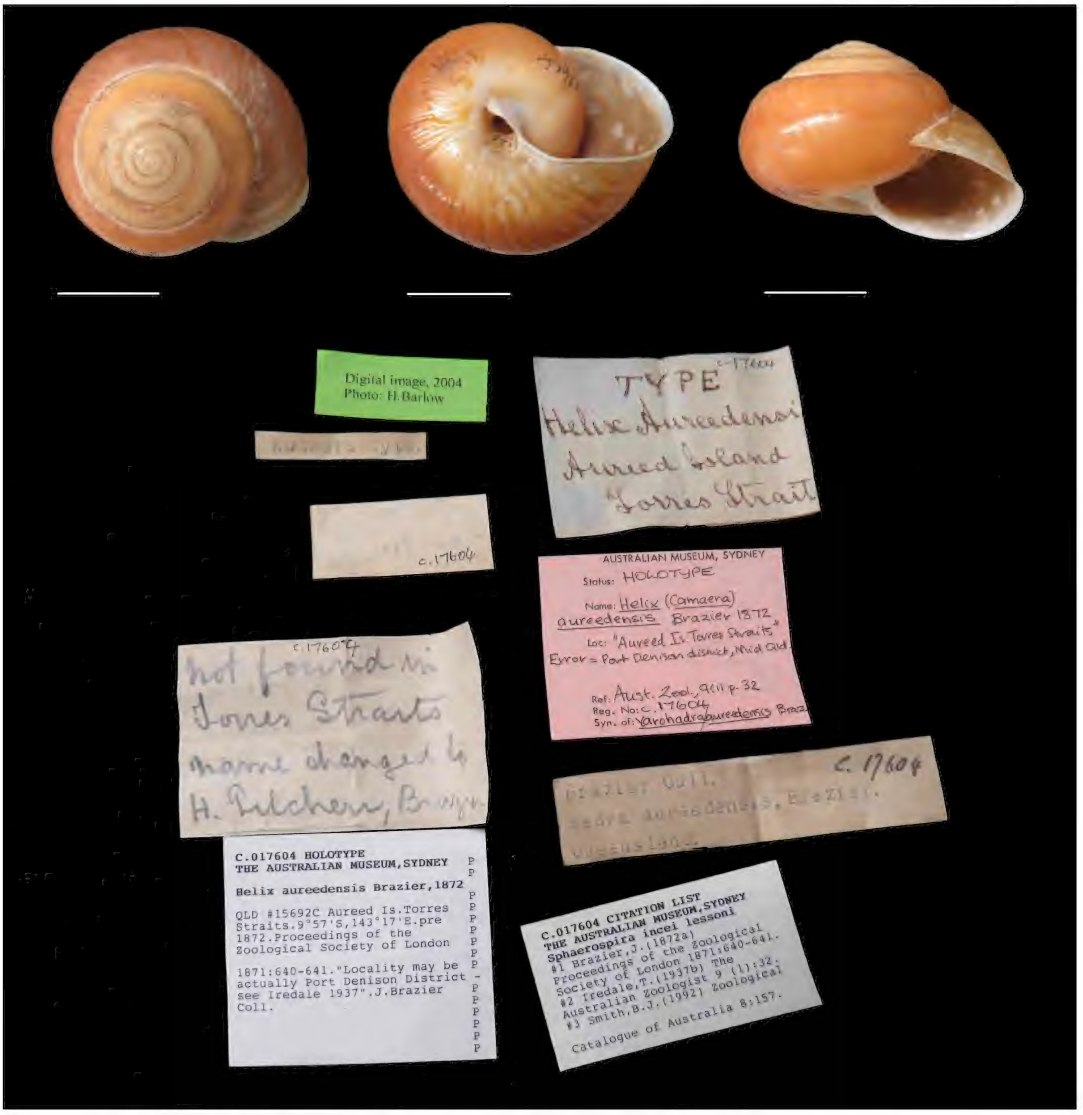
Digital image, 2004
Photo: H.Barlow
TYPE
Helix Aureedensi
Aureed Island
Torres Strait
c.17604
AUSTRALIAN MUSEUM, SYDNEY
Status: HOLOTYPE
Name: Helix (Camaena)
aureedensis Brazier 1872
Loc: "Aureed Is.Torres Straits"
Error = Port Denison district, N'rld Qld
Ref. Aust. Zool. 9(1) p. 32
Reg. No.: C.17604
Syn. of: Varohadra aureedensis Braz.
not found in
Torres Straits
name changed to
H. Pilsbry, Brazier
C.017604 HOLOTYPE
THE AUSTRALIAN MUSEUM, SYDNEY
Helix aureedensis Brazier, 1872
QLD #15692C Aureed Is.Torres Straits.9°57'S,143°17'E.pre 1872.Proceedings of the Zoological Society of London 1871:640-641."Locality may be actually Port Denison District - see Iredale 1937".J.Brazier Coll.
C.017604 CITATION LIST
THE AUSTRALIAN MUSEUM, SYDNEY
Sphaerospira incei lessoni
#1 Brazier,J.(1872) Proceedings of the Zoological Society of London 1871:640-641.
#2 Iredale,T.(1937b) The Australian Zoologist 9 (1):32;
#3 Smith,B.J.(1992) Zoological Catalogue of Australia 8:157.

FIG. 15. *Helix (Camaena) aureedensis* Brazier, 1872, AMSC017604, holotype. Scale bars: 10 mm. Image: JS courtesy of AM.

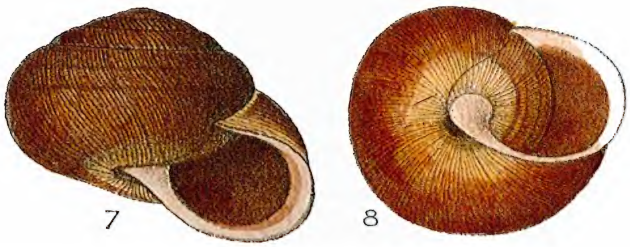

FIG. 16. *Helix (Camaena) aureedensis* Brazier, 1872 as illustrated in Pilsbry (1893, pl. 54, figs 7, 8).

Brazier commented that he had seen similar shells in some of the Australian collections labelled as a variety of *H. incei*, but with no white thread-like line at the suture as in the present species. The fine white sutural thread and yellow circum-umbilical patch are important features of the shell morphology of this species.

Hedley (1888: 102) first questioned the type locality of Aureed Island, saying that Brazier himself had admitted that this could have been the localities around Port Denison. As stated in the 'Background' section, land snails from the Hargraves collection are notorious for inaccuracies in their locality data.

Pilsbry's (1893, pl. 54, figs 7-8) illustration of *Helix (Camaena) aureedensis* also highlighted the yellow circum-umbilical patch that is characteristic of this species (Fig. 16). This shell character is absent in *Helix lessoni*.

Iredale (1937) realised that no species resembling Brazier's description were to be found in the Torres Strait and termed the designation of the type locality as Aureed Island an error, nominating the type locality as the Port Denison district, consistent with Hedley's comment. Port Denison is currently recognised as a small area around Bowen, MEQ, but historically included areas further southward to north of Rockhampton, SEQ. QM and AM collections show that neither this species, nor any other species in the *Figuladra* clade, occurs north of the O'Connell River, south of Proserpine, MEQ.

Smith (1992) included *H. aureedensis* as a synonym of *Sphaerospira incei lessoni* (Pfeiffer, 1846) along with *Varohadra bernhardi* Iredale, 1933 which has been considered a junior synonym of the former. This erroneous classification was followed by Stanisic *et al.* (2010).

Shells aligning with Brazier's description of *H. aureedensis* (including those possessing a fine white sutural thread and yellow circum-umbilical patch) in the QM and AM collections occur in MEQ in the limestone outcrops of Mt Etna NP and along the coast from Emu Park to Yeppoon and north to Sandy Point. Lighter banded forms of the species (= *Helix (Hadra) yeppoonensis* Beddome, 1897) are especially prevalent in the coastal vine thickets in this area. Consequently, these names should only be applied to populations in the greater Yeppoon area and a more suitable type locality nominated as Johannsen's Caves, Mt Etna NP, MEQ where both the dark morph with yellow circum-umbilical patch and the lighter banded morph occur in great abundance.

Helix (Camaena) challisi Cox, 1873

(Figs 17–19)

Cox (1873: 565, pl. 48, Figure 3) described and illustrated *Helix (Camaena) challisi* using specimens from the Hargraves collection occurring on L Island (Fig. 17).

Establishing the probable type localities of species described over 100 years ago has proven difficult with name changes and recording of locations in Queensland as 'Northern Australia', often including the Great Barrier Reef environs as part of Torres Strait. When Cox described *Helix challisi* in 1873, he referred to the type locality as L Island, Torres Strait. Hedley (1888: 102) noted the location as incorrect and said that it should be 'in the neighbourhood of Broadsound, 20° 52′ S, 149° 37′ E'. However, these coordinates are not those of the Broadsound area in MEQ, but rather those of the Scawfell Islands in the South Cumberland island group, MEQ. Iredale (1937) noted that L Island, Torres Strait, did not exist and was an error and considered L Island to be Long Island, Broadsound, SEQ. Once again it would seem that the errant locality data often associated with the Hargraves collection of land snails has been the source of this unintended confusion.

Naming a principal island, or groups of islands, on a map using an alphabetic notation was a custom used by Royal Naval hydrographers of the nineteenth century. Further research revealed 'L Island' as being named by Matthew Flinders in 1802. In his diary of the journey Flinders (1802) wrote:

> 'Friday 15 October, 1802. At eleven we rounded their west end; and at noon were in latitude 20° 38′ 58″, and from the bearing of the Cumberland Isle *k*, in longitude 150° 01′ east. We were now obliged to steer west-

ward again, having reefs at the distance of two miles, from N. E. by E., to N. W. by W.; and seeing that they extended onward, and the breeze was fresh, I hauled up for the Cumberland Island marked *l*, the largest yet seen, with the intention of anchoring there for the night. The tide carried us too far to leeward, but we fetched a lesser island, *l2*, seven miles to the north; and came to, in 17 fathoms grey sand, one mile from a beach on its north-west side, and half a mile from the reef which surrounds the island.'

Flinders noted in the voyage log that *l* islands were the 'S.E. most of the Cumberland Isles as laid down by Captain Cook' (Flinders 1802-1803).

Given the latitudes and longitudes of the time and description of the islands, we submit that Keswick Island is L Island and Brampton Island (7 km north of Keswick Island), is L2 Island. L Island was visited by H.M.S. *Fly*, and altitude data collected by Mr. Evans, the Master of the *Fly* (Jukes, 1842-1846), indicate that he logged L Island in the southern Cumberland Islands.

FIG. 17. Cox's (1873: pl.48, Figure 3) illustration of *Helix (Camaena) challisi*.

Based on the evidence presented above, the type locality of *H. challisi* is herein restricted to Keswick I in the South Cumberland island group.

There has been significant, long-term confusion surrounding the identities of *Figuladra challisi* (Cox, 1873) and *Figuladra mattea* (Iredale, 1933) and mixed groupings exist in both the AM and QM collections. Smith (1992) considered these taxa to represent the same species in *Sphaerospira*. Stanisic *et al.* (2010) followed Iredale (1937) and treated them as separate

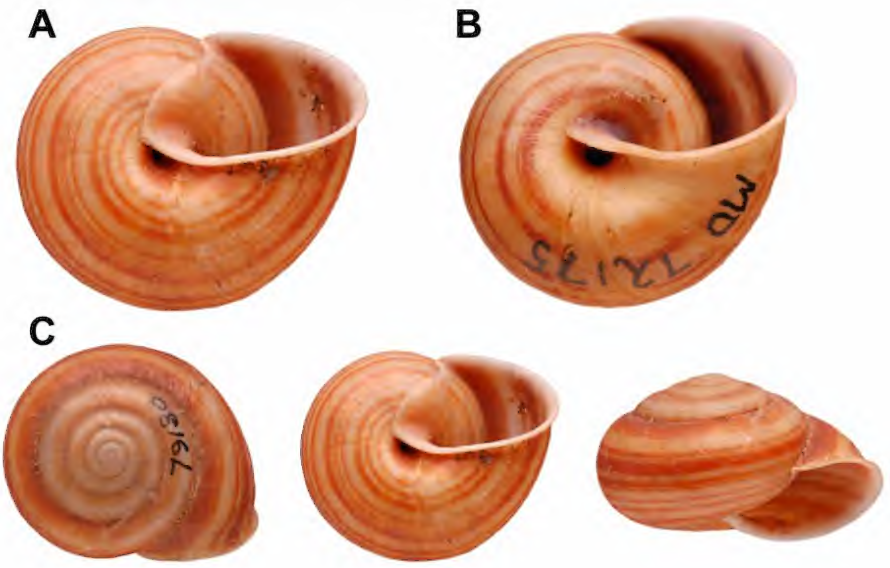

FIG. 18. A-B. Comparison of umbilical areas. **A,** *Figuladra challisi,* AMSC 79130, Keswick I., MEQ; **B,** *F. mattea,* QMMO72175, Bracewell, SEQ. **C,** *Figuladra challisi* illustrated in Stanisic *et al.* (2010: species 758, AMSC79130, Keswick I, MEQ. Images A, C: from Stanisic *et al.* (2010).

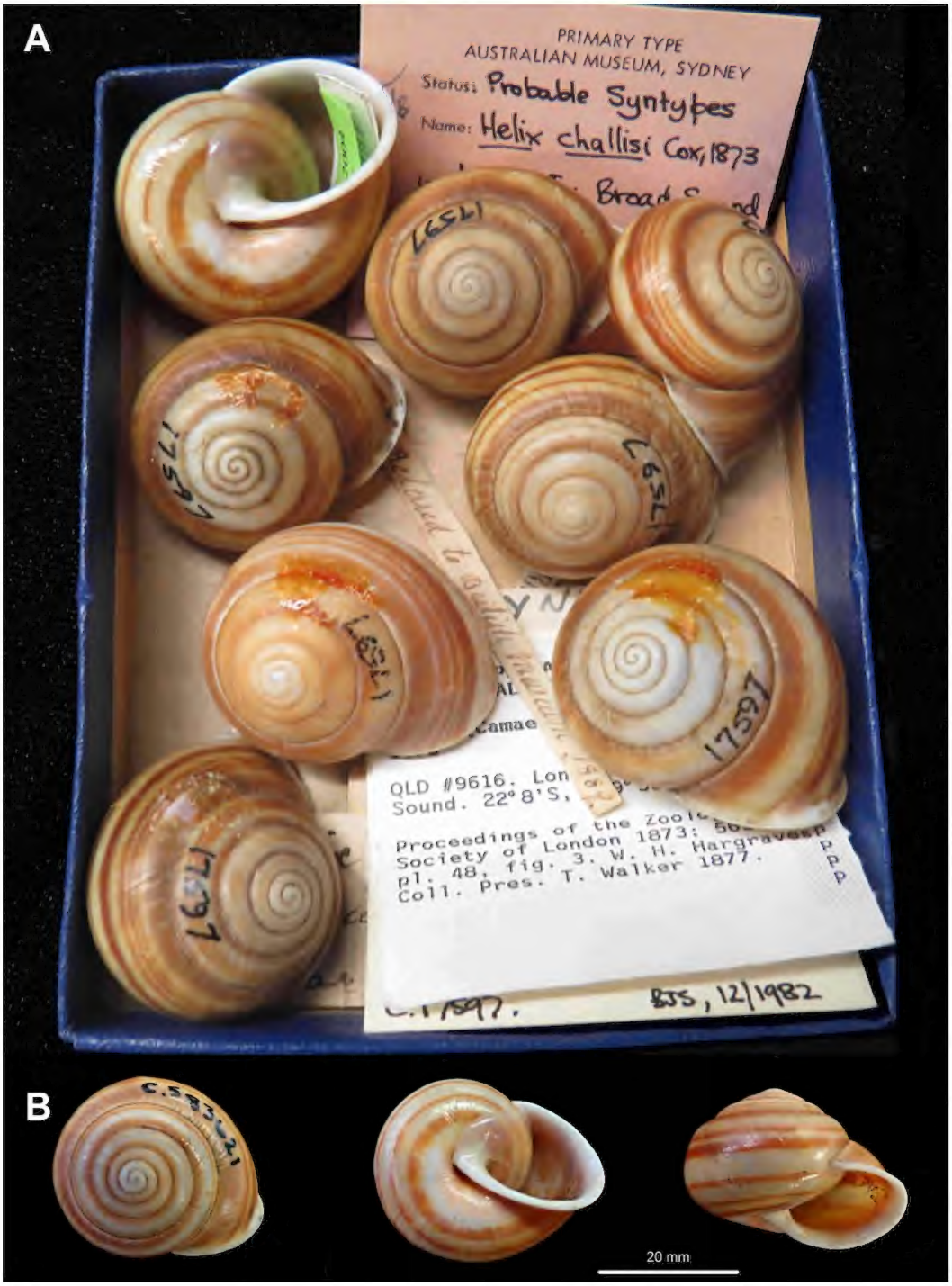

FIG. 19. *Helix (Camaena) challisi* (Cox, 1873). **A,** AMSC 17597, probable syntypes as cited by Smith (1992). **B,** lectotype, AMSC583621, Keswick I, MEQ. Scale bar: 20 mm. Images: A. AM; B JS courtesy of AM.

species but then re-assigned both to *Figuladra*. The two species have. They have very similar shell morphologies, though *F. mattea* differs from *F. challisi* chiefly by having a more solid shell and a more excavate umbilical region (Figs 18A, B). *Figuladra challisi* has a flatter, 'ceramic-like' shell as illustrated in Stanisic *et al.* (2010) from a specimen from Keswick Island, MEQ (Fig. 18C). *Figuladra mattea* is an open woodland snail found between Brisbane and Rockhampton, SEQ (type locality Rockhampton) whereas *H. challisi* is a vine thicket dweller. Confirmation of the type locality of *F. challisi* as Keswick Island in MEQ indicates that the two species are geographically separated.

Cox (1873) did not designate a holotype for *H. challis*. Smith (1992) recorded eight probable syntypes from L Island in the AM (AMSC17597) from the Hargraves collection (Fig. 19A). While the most recent labels with these specimens indicate that Long I, Broadsound is their collection locality, a handwritten label by Cox shows that these specimens are from L Island, Torres Strait, the original type locality associated with Cox's description. Accordingly, these shells are considered to be the original type series. As a result, a lectotype (AMSC583621) is designated from this series (Fig. 19B).

DISCUSSION

The historical taxonomic confusion surrounding *Figuladra* species described prior to 1900 encompasses a range of outstanding issues outlined in this study. These have been resolved through an examination of type and related specimens and their reconciliation with original descriptions and illustrations. In some cases, this meant scrutinising the logs of the early expeditions of exploration and those of individual collectors. In many instances, purported types were shown to be wrongly designated and the true type species or series are presumed lost.

The key decisions resulting from this study outlined below:

A single shell of *Helix incei* Pfeiffer (in Philippi), 1846 collected by Commander Ince RN and considered part of the original type series was located in the NHMUK. This specimen (NHMUK20200001) is herein designated as lectotype and the type locality fixed as the Percy Islands, MEQ. *Helix incei* should only apply to Percy Island populations.

The subsequently designated type locality of the Percy Islands, MEQ for *Helix lessoni* Pfeiffer, 1846 by Iredale (1937) is considered an error and is herein amended to Port Curtis. No type material corresponding to Pfeiffer's original description of this species is considered to exist in the NHMUK. A lectotype (ZMB/Moll 260025a) and a paralectotype (ZMB/Moll 260025b) from Pfeiffer's personal collection in the ZMB are designated herein. *H. lessoni* should only apply to populations in the Port Curtis area.

A specimen from the personal collection of George French Angas in the Hancock Museum, Newcastle on Tyne (NEWHM:HANM.1.3531) is confirmed as the holotype of *Helix curtisiana* Pfeiffer, 1864 with the original broad type locality of Port Curtis. This type locality is further restricted herein to Boyne I, MEQ. *H curtisiana* should only apply to populations in the immediate Port Curtis area.

The original type locality for *Helix (Camaena) praetermissi* Cox, 1868 (holotype AMSC17600) of Cape Direction, NEQ is considered an error and is amended to the Keppel Islands, MEQ. *H. praetermissi* should only apply to populations on the Keppel Islands pending the outcome of future studies.

The original type locality for *Helix (Camaena) aureedensis* Brazier, 1872 (holotype AMSC017604) of Aureed Island, Torres Strait, is considered an error and is amended to a locality in the Yeppoon area, MEQ. Johannsen's Caves, Mt Etna NP, MEQ is herein nominated. *Helix aureedensis* should only apply to populations in the greater Yeppoon area.

The original type locality of L Island, Torres Strait, and subsequent redesignated type locality of L Island, Broadsound, MEQ for *Helix (Camaena) challisi* Cox, 1873 are considered errors and the type locality is amended herein to Keswick Island, MEQ. A lectotype (AMSC583621) and

seven paralectotypes (AMSC17597) are herein designated from what is considered to be the original type series studied by Cox. *H. challisi* should only apply to Keswick Island populations pending the outcome of future studies.

The above decisions have been taken to stabilise the taxonomy of these species and allow for a comprehensive revision of *Figuladra* Kohler & Bouchet, 2020 to be undertaken unencumbered by nomenclatural uncertainty.

These findings are the outcome of detailed investigative work by the senior author and will be further amplified in a forthcoming revision of the *Figuladra* clade.

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LITERATURE CITED

Adams, H. & Angas, G. F. 1864. Descriptions of new genera and species of Chitonidae from the Australian seas, in the collection of George French Angas. *Proceedings of the Zoological Society of London,* **32:** 192-194.

Adams, H. & Angas, G. F. 1865. Descriptions of two new species of shells in the collection of George French Angas. *Proceedings of the Zoological Society of London,* **33**(1): 54-54. https://doi.org/10.1111/j.1469-7998.1865.tb02307.x

Angas, G. F. 1865. On the marine molluscan fauna of the Province of South Australia, with a list of all the species known up to the present time, together with remarks on their habitats and distribution, etc. Proceedings of the Zoological Society of London, 1865, 155-180.

Angas, G. F. 1867. A list of species of marine Mollusca found in Port Jackson harbour, New South Wales, and on the adjacent coasts, with notes on their habits, etc. Part I. *Proceedings of the Zoological Society of London*, **1867**, 185-233.

Angas, G. F. 1878. Description of a new Species of Tudicula. *Proceedings of the Zoological Society of London*, **1878**, 610-611. https://doi.org/10.1111/j.1469-7998.1878.tb07992.x

Bishop, M. J. 1978. A Revision of the Genus Thersites Pfeiffer (Pulmonata: Camaenidae). *Journal of the Malacological Society of Australia*, **4,** 9-21. https://doi.org/10.1080/00852988.1978.10673904

Bramley, E., Zilio, F. & Gardam, L. 2008. *George French Angas Guide to Records* [Online]. Sydney: South Australian Museum Archives. Available: http://archives.samuseum.sa.gov.au/aa8/provlist.htm [Accessed 6 February, 2020].

Brazier, J. 1872. Descriptions of eight new Australian Land-Shells. *Proceedings of the Royal Society of London*, **41**, 639-642.

Calaby, J. H. 1967. MacGillivray, John (1821–1867) [Online]. Australian National University. Available: http://adb.anu.edu.au/biography/macgillivray-john-2401/text3173, published first in hardcopy 1967 [Accessed 20 April, 2020].

Chimmo Rn, C. 1855. Shipping Intelligence. *The Moreton Bay Courier*, 3 March.

Cox, J. C. 1868. *Monograph of Australian Land Shells,* (Sydney: William Maddock).

Cox, J. C. 1873. Descriptions of new species of land and marine shells from Australia and the Solomon and Louisiade Islands. *Proceedings of the Zoological Society of London,* **1873**, 564-569.

Dance, S. P. 1980. Hugh Cuming (1791-1865) Prince of collectors. *Proceedings of the Zoological Society of London,* **9**, 477-501. https://doi.org/10.3366/jsbnh.1980.9.PART_4.477

Flinders, M. 1802. Book 2: Transactions during the Circumnavigation of Terra Australis, from the time of leaving Port Jackson to the return to that port [Online]. South Australia: University of South Australia. Available: https://ebooks.adelaide.edu.au/f/flinders/matthew/voyage-to-terra-australis/complete.html#book2 [Accessed 23 April 2019].

Flinders, M. 1802-1803. *Journal on the Investigator* [Online]. Available: http://acms.sl.nsw.gov.au/_transcript/2012/D15343/a056.html [Accessed 9 September 2019].

Hedley, C. 1888. A list of land shells recorded from Queensland. *Proceedings of the Royal Society of Queensland*, **5,** 45-70.

Hedley, C. 1912. *Conchological Chat from London. Nautilus*, **26** (8), 85-88.

Hedley, C. 1913. Studies on Australian Mollusca. Part XI. *Proceedings of the Linnean Society of New South Wales,* **38,** 258-339. https://doi.org/10.5962/bhl.part.13561

Hedley, C. & Musson, C. T. 1892. On a collection of land and freshwater shells from Queensland. *Proceedings of the Linnean Society of New South Wales,* **6** (3), 551-564. https://doi.org/10.5962/bhl.part.29904

ICZN 2012. International Code of Zoological Nomenclature *In:* Ride, W. D. L., Cogger, H. G., Dupuis, C., Kraus, O., Minelli, A., Thompson, F. C. & Tubbs, P. K. (eds.) 4 ed. London: *The International Trust for Zoological Nomenclature.*

Iredale, T. 1933. Systematic notes on Australian land shells. *Records of the Australian Museum*, **19,** 37–59. https://doi.org/10.3853/j.0067-1975.19.1933.690

Iredale, T. 1937. A basic list of the land Mollusca of Australia.-Part II. *The Australian zoologist.*, **9,** 1-39.

Iredale, T. 1959. George French Angas: The father of Australian conchology. *Supplement to The Australian Zoologist,* **12,** 362-371.

Jukes, J. B. 1847. *Narrative of the Surveying Voyage of HMS Fly: During the Years 1842–1846*, Vol. 1, London, T. W. Boone.

Köhler, F. & Bouchet, P. 2020. On unavailable genus-group names introduced by Tom Iredale for Australian non-marine gastropods: nomenclatural clarifications and descriptions of new genera, *Molluscan Research,* **40**: 2, 150-159. https://doi.org/10.1080/13235818.2020.1724603

Macgillivray, J. 1851. *Narrative of The Voyage Of H.M.S. Rattlesnake, Commanded By The Late Captain Owen Stanley, R.N., F.R.S. Etc. During The Years 1846-1850.* London, T. W. Boone. https://doi.org/10.5962/bhl.title.12974

Morgan, E. J. R. 1966. Angas, George French (1822–1886). *Australian Dictionary of Biography,* National Centre of Biography, Australian National University. (Australia: Melbourne University Press).

Pilsbry, H. A. 1893. *Manual of conchology: structural and systematic.* VIII, Philadelphia, Academy of Natural Sciences of Philadelphia.

Pfeiffer, L. 1846a. Description of thirty-six new species of Helix from the collection of Hugh Cuming esq. *Proceedings of the Zoolological Society of London*, **8**, 126-136.

Pfeiffer, L. 1846b. Symbolae ad historiam heliceorum 3, Cassellis, Sumptibus & typis Th. Fischeri.

Pfeiffer, L. 1864. Descriptions of ten new species of land-shells, from the collection of George French Angas, Esq. *Proceedings of the Zoological Society of London*, 1863, 526-529.

Pfeiffer, L. G. K. 1846b. Symbolae ad historiam heliceorum 3, Cassellis, Sumptibus & typis Th. Fischeri.

Philippi, R. A. 1846 ('1845'). Abbildungen und Beschreibungen neuer oder wenig gekannter *Conchylien unter Mithülfe meherer deutscher Conchyliologen*. Cassel, T. Fischer. https://doi.org/10.5962/bhl.title.10589

Pilsbry, H. A. 1890. *Manual of conchology: structural and systematic. VI: Guide to the study of helices.*, Philadelphia, Academy of Natural Sciences of Philadelphia.

Poppe, G. T. & Poppe, P. 1994. *Shellers From the Past and the Present: George French Angas* [Online]. Conchology Inc. Available: https://www.conchology.be/?t=9001&id=14630 [Accessed 6 February, 2020].

Reeve, L. A. 1854. Monograph of the genus *Helix*. *In*, Reeve, L. A. (ed.) *Conchologia Iconica,* 7: 210 plates, 1495 species (without pagination). London [publication dates: pls 1–62 - 1851; pls 63-146 - 1852; pls 147–174 - 1853; pls 175–210 - 1854].

Smith, B. J. 1992. Non-marine Mollusca. *In,* HOUSTON, W.W.K.E. (ed.) *Zoological Catalogue of Australia.* Australian Government Publishing Service.

Tryon, H. 1888. Errata contained in a "List of the Land Shells Recorded from Queensland". *Proceedings of the Royal Society of Queensland,* **5** (4), 131-137.

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New species and genera of Pinwheel Snails from the brigalow lands of south central Queensland (Gastropoda: Eupulmonata: Charopidae)

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ABSTRACT

Six new genera and 15 new species of Charopidae are described from the brigalow lands of south central Queensland (SCQ) as follows: *Rhophodon moffatt* sp. nov., *Tristanoropa saddler* sp. nov., *Tristanoropa crowman* sp. nov., *Tristanoropa palmgrove* sp. nov., *Brigaloropa costulata* gen. et sp. nov., *Arcadiaropa sunnyholt* gen. et sp. nov., *Eddiea carnarvon* gen. et sp. nov., *Eddiea waddybrae* gen. et sp. nov., *Eddiea oakwells* gen. et sp. nov., *Eddiea bigge* gen. et sp. nov., *Platyumbiropa grafton* gen. et sp. nov., *Platyumbiropa tabor* gen. et sp. nov., *Carnaropa racecourse* gen. et sp. nov., *Carnaropa salvatorosa* gen. et sp. nov. and *Cineropa roma* gen. et sp. nov. *Elsothera hewittorum* Stanisic, 1996 previously only known from Mt Rose Station, via Taroom, SCQ is given a slightly expanded range and reassigned to *Cineropa* gen. nov.; the range of *Spiraliropa carnarvon* Stanisic, 2010 described from the Carnarvon Ranges is greatly expanded to cover more of the SCQ area; and additional new SCQ locality records are provided for the continentally widespread *Discocharopa aperta* (Möllendorff, 1888).

❑ *Mollusca, Eupulmonata, Charopidae, south central Queensland, protoconch sculpture, new genera, new species.*

Pinwheel Snails (Charopidae) from the semi-arid Brigalow Lands Bioregion of South Central Queensland (hereafter SCQ, roughly 23°30'-26°00'S × 146°30'-149°30'E) have historically been poorly represented among the Queensland Museum (QM) land snail collections. Consequently, up to the present only two species, *Elsothera hewittorum* Stanisic, 1996 and *Spiraliropa carnarvon* Stanisic, 2010 have been described from this relatively vast and semi-arid region.

In October 2014 the author was invited to participate in a Bush Blitz land survey (see 'Acknowledgements') on Carnarvon Station Reserve, SCQ that led to the collection of a small number of charopid species from vine thicket habitats including some new species. Shortly thereafter, Roma-based malacologist and environmental consultant Craig Eddie donated 65 lots of assorted SCQ charopids to the QM. These specimens, accumulated over many years from diverse localities and habitats (chiefly vine thickets) in SCQ, included a number of additional species identified as new to science.

The aim of this study was to document these new species from a region greatly damaged by land clearing in the past and currently under threat from mining development.

Six genera and fifteen species of Charopidae from the brigalow region of SCQ are described as new; the previously described *Elsothera hewittorum* Stanisic, 1996 is reassigned to a new genus with additional records documented for the species; and additional distribution data in SCQ are provided for the regionally endemic *Spiraliropa carnarvon* Stanisic, 2010 and the wide-ranging *Discocharopa aperta* (Möllendorff, 1888).

MATERIAL AND METHODS

This study, with a single exception, is based on material housed in the Queensland Museum's land snail collections (QMMO). One lot from the Salvator Rosa Section of Carnarvon NP, SCQ is from the Australian Museum, Sydney (AMSC). Apart from several lots of preserved snails this material is comprised chiefly of dead shells covering a range of age classes (mostly juvenile and sub-adult) recovered from leaf litter sorting. Investigations of shell characters are confined, with one exception, to specimens with greater than 4.0 whorls which designates an adult snail. Characters scored include shell height and diameter, protoconch whorl numbers and diameter, whorl count, rib count on the first whorl and umbilical width. Whorl counts were made to the nearest 1/8 whorl following Solem (1983). Specimens were studied using a WILD M5 stereo microscope. High resolution images of shells were obtained using a Visionary Digital BK-Plus lab system camera set-up located in the Queensland Museum's Digital Imaging Unit. Shell sculpture was investigated and photographed using a TM-1000 Tabletop Scanning Electron Microscope (SEM) located in the Queensland Museum.

Due to the fragile nature of many of the specimens recovered by sorting leaf litter, only limited ultrasonic cleaning of shells was attempted in most cases. Hence, many of the illustrated specimens remain covered in fine dirt particles. This shortcoming in presentation however, should not interfere with species' identifications.

Abbreviations. alt, altitude; AM, Australian Museum, Sydney; Ck, Creek; Mt, Mountain; MV, Museum of Victoria; NP, National Park; NSW, New South Wales; NENSW, north-eastern New South Wales; NEQ, north-eastern Queensland; MEQ. mid-eastern Queensland; NP, National Park; R, River; Ra, Range; RC, dry collection; SC, spirit collection; SCQ, south-central Queensland; SEM, scanning electron microscopy; SEQ, south-eastern Queensland; sevt, semi-evergreen vine thicket; SF, State Forest; Stn, Station.

Generic differentiation and species delimitation

Holcroft (2018a) established a framework for utilising protoconch sculpture as a means of recognising putative charopid genera in the absence of soft parts for the study of reproductive structures and DNA analyses. This protoconch framework, adopted in this study, is considered to produce a more systematic grouping of species' clusters (genera) than has previously been the case. The underlying hypothesis is that protoconch architecture as part of the embryonic shell formed in the egg, is more likely to be an indicator of close relationships between species than the post-hatched teleoconch (adult shell) which is formed subject to varying environmental pressures. The study of Shea *et al.* (2012) has already shown that there is a strong genetic basis for such an approach.

Hence, the new genera introduced in this study are diagnosed on differences in protoconch sculptures, some previously documented but many new. The protoconch sculptures that define the new genera are considered distinctive and unique among the many sculptural patterns documented in previous studies thus far (Stanisic 1990; Hyman & Stanisic 2005; Shea *et al.* 2012; Stanisic 2016; Holcroft 2018 a,b,c; Holcroft & Stanisic 2018). In many cases, they are based on subtle interpretation of sculptural architecture that is visible only by SEM. Charopids are inherently rich in shell characters and consequently new species have been diagnosed on the basis of the protoconch sculpture combined primarily with coiling pattern, shell shape, apertural barrier formation and teleoconch sculpture.

SYSTEMATICS

Order EUPULMONATA

Superfamily PUNCTOIDEA

Family CHAROPIDAE

Spiraliropa Stanisic, 2010

Spiraliropa Stanisic, 2010 (in Stanisic *et al.* 2010): 256.

Type species. *Spiraliropa carnarvon* Stanisic, 2010-by original designation.

Diagnosis. Shell tiny, brown, discoidal with a flat spire; whorls rounded, sutures strongly impressed; protoconch spiral consisting of 12-13 widely spaced, slender, high spiral cords; teleoconch sculpture of crowded, slightly irregularly spaced, bladed radial ribs, microsculpture of fine radial threads and low spiral cords; umbilicus wide, V-shaped.

Remarks. *Spiraliropa* Stanisic, 2010 is readily distinguished among the SCQ charopid genera hitherto diagnosed by the combination of tiny brown shell, protoconch with 12—13 widely spaced, slender spiral lirae and teleoconch with crowded and bladed radial ribs. The protoconch sculpture bears a strong similarity to that of *Comularopa* Holcroft, 2018 described from the highland rainforests of the Clarke Range, MEQ (Holcroft 2018b). A significant difference between the two genera is the structure of the spiral cords on the protoconch which are more slender, almost flimsy, in *S. carnarvon* when compared with the slightly broader and more robust cords of both *C. georginae* Holcroft, 2018 and *C. wendyae* Holcroft & Stanisic, 2018.

Spiraliropa carnarvon Stanisic, 2010
(Figs 1A-B, 6A-B)

Spiraliropa carnarvon Stanisic, 2010 (in Stanisic *et al.* 2010): 256.

Common name. Carnarvon Pinwheel Snail.

Material examined. All SCQ. Holotype. QMMO66493, Carnarvon NP, Mt Moffatt Section, summit of Mt Moffatt, SCQ, 25° 03′ 33″ S, 148° 02′ 36″ E, vine thicket, coll. C. Eddie, 4.ix.1999. Height of shell 1.64 mm, diameter 3.28 mm, width of umbilicus 1.23 mm, D/U 2.67, H/D 0.50, whorls 3.875.

Paratypes. QMMO78979, 3RC, same data as holotype; QMMO65348, 4RC, Carnarvon NP, Mt Moffatt Section, N Marlong Arch plain, 24° 53′ 54″ S, 147° 58′ 07″ E, woodland/vine thicket, coll. C. Eddie, G. Enerver, 27.xi.1996.

Other material. QMMO23488, 8SC/2RC, Blackdown Tableland NP, Rainbow Falls Walk, 23° 49′ S, 149° 05′ E, wet sclerophyll with ferns/palms, under logs, coll. J. Stanisic, D. Potter, J. Chaseling; QMMO66440, 2RC, Lonesome NP, Arcadia Valley Rd, 25° 29′ 26″ S, 148° 48′ 58″ E, brigalow woodland, coll. C. Eddie, 27.v.1999; QMMO65316, 1RC, Taroom, NW at Expedition NP, Amphitheatre Section, 25° 12′ 24″ S, 148° 59′ 18″ E, sevt, under logs, coll. C. Eddie, G. Annabell, 26.v.1998; QMMO86616, 5RC, Injune, 48 km NNE at Hilly Vale Stn, Arcadia Valley, 25° 28′ 41″ S, 148° 49′ 34″ E, sevt/Brachychiton on sandstone, in leaf litter/under and in logs, coll. C. Eddie, 20.i.2004; QMMO86569, 2RC, 36.7 km ENE at Moonah Stn, 25° 43′ 49.1″ S, 148° 54′ 43.4″ E, sevt on sandstone, in leaf litter/under and among rocks, coll. C. Eddie, 09.xi.2011; QMMO86601, 1RC, Injune, 50.1 km NE at Lonesome Holding, NE end of Mt Jiman, 25° 29′ 23″ S, 148° 52′ 47″ E, depauperate sevt on sandstone, in leaf litter/under and among rocks, coll. C. Eddie, 16.xii.2003; QMMO86612, 19RC, Carnarvon NP, Mt Moffatt Section, N side Mt Moffatt peak, 25° 03′ 24″ S, 148° 02′ 41″ E, sevt/basalt scree, in litter among rocks, coll. C. Eddie, 13.x.2002; QMMO86821, 6RC, Carnarvon NP, Mt Moffatt Section, ridge NW Lots Wife, SCQ, 24° 56′ 00″ S, 148° 05′ 43″ E, sevt/sandstone, in litter, coll. C. Eddie, 22.i.1999; QMMO56641, 1RC, Carnarvon NP, beginning of gorge walk, 25° 03′ 25″ S, 148° 13′ 30″ E, palms/ferns on sandstone, under logs and rocks, coll. J. Stanisic, D. Potter, 20.ix.1995; QMMO80597, 1RC, Carnarvon NP, track to Amphitheatre, Carnarvon Gorge, 25° 03′ 25″ S, 148° 13′ 30″ E, coll. G. Annabell, 8.vi.1986; QMMO86568, 4RC, Carnarvon NP, Mt Moffatt Section, on ridge west of Marlong Plain, 24° 57′ 33″ S, 147° 56′ 48″ E, brigalow woodland, in leaf litter, under/among rocks, coll. C. Eddie, 04.ii.2000; QMMO86604, 4RC, Carnarvon NP, Mt Moffatt Section, gully on W side of Gee Gee Gap Rd, 24° 56′ 55″ S, 147° 54′ 10″ E, sevt on sandstone, coll. C. Eddie, 03.iv.1996; QMMO80718, 3RC, Carnarvon Stn, 24° 43′ 44.9″ S, 147° 46′ 14.0″ E, sevt, under rocks and logs in litter, coll. J. Stanisic, L. Holcroft, 26.ix.2012; QMMO80225, 4RC, QMMO80121, 49RC, Carnarvon Stn, rocky knoll NW homestead, 24° 46.007′ S, 147° 43.533′ E, ironbark woodland/basalt scree, coll. J. Stanisic, 10.x.2014; QMMO80260, 1RC, QMMO80257, 5RC, Carnarvon Stn, N homestead, 24° 47.935′ S, 147° 45.284′ E, vine thicket/basalt scree, coll. J. Stanisic, 13.x.2014; QMMO80217, 9RC, Carnarvon Stn, NW homestead, 24° 46.008′ S, 147° 44.530′ E, vine thicket on rocky slope, coll. J. Stanisic, 9.x.2014; QMMO80117, 5RC, Carnarvon Stn, Conglomerate Spring, 24° 50.383′ S, 147° 46.973′ E, eucalypt

woodland, coll. J. Stanisic , 8.x.2014; QMMO86605, 6RC, Augathella, 158 km NE at Carnarvon Stn, 24° 48′ 04″ S, 147° 43′ 49″ E, sevt on basalt, in leaf litter/ under rocks, logs and base of figs, coll. C. Eddie, W. McDonald, 13.iv.2004; QMMO86603, 48RC, Augathella, 161 km NE at Carnarvon Stn, 24° 48′ 40″ S, 147° 46′ 30″ E, sevt on quartzite, in leaf litter/ under rocks and logs, coll. C. Eddie, W. McDonald, 16.iii.2004; QMMO86575, 47RC, Augathella, NE at Mt Tabor Stn, E slope of Urandoo, 25° 13′ 46″ S, 147° 31′ 50″ E, sevt on basalt, in leaf litter/under rocks and logs, coll. C. Eddie, W. McDonald, 22.iv.2004; QMMO86630, 107RC, Augathella, NE at Mt Tabor Stn, ENE of Urandoo, 25° 11′ 45″ S, 147° 30′ 59″ E, sevt on basalt, in leaf litter/among rocks, coll. C. Eddie, R. Alsthorpe, 24.x.2015; QMMO86580, 15RC, Yuleba, 16.5 km SW at Silver Valley Stn, 26° 44′ 10.7″ S, 149° 17′ 18.8″ E, sevt regrowth on laterite, under rocks/in leaf litter, coll. C. Eddie, A. Hoffmann, 04.01.2015; QMMO86563, 3RC, QMMO86631, 3RC, Miles, 40.6 km NW at Gurulmundi SF, 26° 24′ 34″ S, 149° 53′ 05″ E, Ficus on laterite, among leaf litter around fig roots and between boulders, coll. C. Eddie, 17.vii.2014; QMMO86581, 1RC, 'Rossmore', 8.6 km NW of Dulacca, 26° 36′ 34″ S, 149° 40′ 55″ E, open forest, among soil under log. coll. R. Johnson, A. Bendall, 07.xi.2013; QMMO79454, 3RC, Stones Country Resource Reserve, 26° 23′ 24″ S, 149° 52′ 50″ E, sevt/ooline, under logs, coll. C. Eddie, 30.vi.2003.

Diagnosis. As for genus.

Description. Shell tiny, brown, discoidal with a flat, shiny spire; whorls rounded, sutures strongly impressed; diameter 2.46-3.54 mm (mean 2.88 mm), height 1.31-1.97 mm (mean 1.45 mm), H/D 0.43-0.56 (mean 0.51): protoconch spiral, diameter 570 µm, sculptured with 12-13 widely spaced, slender, high spiral cords; teleoconch sculpture of crowded, slightly irregularly spaced, bladed radial ribs 56-90 (mean 76) on first whorl; microsculpture of fine radial threads and low, broad spiral cords forming elongate beads at their intersection; aperture ovately lunate; umbilicus wide, V-shaped, diameter 0.90-1.48 mm (mean 1.18 mm), D/U 2.20-3.08 mm (mean 2.45 mm). Based on 32 measured specimens (QMMO66493[1], QMMO78979[2], QMMO86612[4], QMMO80117[2], QMMO86630[10], QMMO86603[4], QMMO80121[4], QMMO57095[2], QMMO86580[3]).

Distribution and habitat. From Blackdown Tableland in the north to Yuleba and Gurulmundi in the south, SCQ; living under forest debris (rocks and timber) in vine thicket and brigalow woodland.

Remarks. *Spiraliropa carnarvon* Stanisic, 2010 is the most widespread charopid species investigated in the current study. Although there is some variation in the shell size of different populations this variability is also present within populations. Originally described from the Carnarvon Ranges, the range of this species is herein extended to include parts of the Expedition Range in the north, Mt Tabor and Yuleba in the south-west and south respectively.

Rhophodon Hedley, 1924

Rhophodon Hedley, 1924: 219; Iredale, 1937: 329; Iredale, 1941: 2; Kershaw, 1955: 30; Burch, 1976: 133; Smith & Kershaw, 1979: 175; Stanisic, 1990: 114; Smith, 1992: 202; Hyman & Stanisic, 2005: 222; Stanisic *et al.*, 2010: 234; Stanisic *et al.*, 2018: 168.

Type species. *Rhophodon peregrinus* Hedley, 1924-by original designation.

Diagnosis. Shell minute to tiny, discoidal; brown occasionally light straw-yellow with brown radial streaks and suffusions; whorls tightly coiled, sutures impressed; protoconch radial with bold radial ribs, becoming more crowded toward the protoconch-teleoconch boundary and weak, moderately spaced, short discontinuous spiral wrinkles; teleoconch sculpture of crowded radial ribs; umbilicus wide cup to saucer-shaped; apertural barriers present.

Remarks. Hedley (1924) introduced *Rhophodon* for three Australian charopids with apertural barriers. Iredale (1941) later removed *Rhophodon contortus* Hedley, 1924 and placed it in a new genus *Letomola* on the basis of differences in barrier formation and protoconch sculpture. Stanisic (1990) synonymized the Victorian *Egilodonta* Iredale, 1937 with *Rhophodon* and added four additional new species from NENSW and SEQ. Subsequently Hyman & Stanisic (2005) added a further four new species from NENSW but removed *Egilodonta* from the synonymy of *Rhophodon*. The species below is included in *Rhophodon* because it conforms to the current concept of the genus in all respects. The discovery of a species of *Rhophodon* in the moist refugia of the Carnarvon Ranges suggests

possible past connections with rainforests further east. A similar biogeographic pattern is seen in the camaenid genus *Mussonena* (see Stanisic *et al*. 2010).

Rhophodon moffatt sp. nov.
(Figs 1C-D, 6C-D)

Etymology. Named for the Mount Moffatt Section, Carnarvon NP, SCQ.

Preferred common name. Mount Moffatt Pinwheel Snail.

Material examined. All SCQ. Holotype. MO86600, RC, Carnarvon NP, Mount Moffatt Section, gorge downstream of Racecourse Spring, 24° 56′ 04″ S, 148° 05′ 49″ E, woodland with vines on basalt scree, in leaf litter among rocks, coll. C. Eddie, 18.ii.2001. Height of shell 0.82 mm, diameter 1.72 mm, width of umbilicus 0.82 mm, D/U 2.10, H/D 0.48, whorls 4.50.

Paratypes. QMMO86540, 5RC, same data as holotype; QMMO86614, 16RC, Carnarvon NP, Mount Moffatt Section, on N side of Mt Moffatt peak, 25° 03′ 24″ S, 148° 02′ 41″ E, sevt on basalt scree, in leaf litter among rocks, coll. C. Eddie, 13.x.2002.

Other material. QMMO66490, 4RC, Carnarvon NP, Mount Moffatt Section, at Racecourse Spring, 24° 56′ 00″ S, 148° 05′ 43″ E, coll. C. Eddie, 22.i.1999; QMMO86598, 1RC, Carnarvon NP, Mount Moffatt Section, gorge downstream of Foley's Spring, 24° 57′ 17″ S, 148° 09′ 57″ E, basalt gorge with tree ferns, in leaf litter among rocks, coll. C. Eddie, 12.xii.2002; QMMO86570, 8RC, Carnarvon NP, Moolayember Section, at Moolayember Gorge, 25° 12′ 13″ S, 148° 23′ 19″ E, dry rainforest on sandstone, in leaf litter from under rock and inside logs, coll. C. Eddie, 12.iv.2004; QMMO86610, 48RC, Injune 95 km NNW at Saddler Springs Stn, 25° 04′ 48″ S, 148° 07′ 27″ E, alt. 820m, vine ticket on basalt scree, in soil/leaf litter among rocks, coll. C. Eddie, 11.xii.2008; QMMO79444, 3RC, Saddler Springs Stn, Carnarvon Range, NW Injune, 25° 04′ 48″ S, 148° 07′ 27″ E, vine thicket on basalt scree, coll. C. Eddie, 11.xii.2008.

Diagnosis. Shell tiny, discoidal with a flat spire, whorls tightly coiled; protoconch radial with bold radial ribs and weak, moderately spaced, short discontinuous spiral wrinkles, teleoconch with moderately crowded radial ribs (mean 52 on first whorl) and numerous interstitial microradial threads; umbilicus wide cup-shaped; six apertural barriers present.

Description. Shell tiny, golden-brown, discoidal with a flat spire; whorls 4.125-4.50 whorls, tightly coiled, sutures impressed; diameter 1.56-1.96 mm (mean 1.75 mm), height 0.66-0.90 mm (mean 0.70 mm), H/D 0.40-0.50 (mean 0.45); protoconch radial, mean diameter 430 μm, sculptured with moderately spaced, bold radial ribs that tend to be more crowded at the protoconch-teleoconch boundary and weak, moderately spaced, short discontinuous spiral wrinkles; teleoconch sculpture of moderately crowded radial ribs 48-55 (mean 52) on first whorl, microsculpture of fine crowded microradial threads (8-10 between each major rib) continuous on the major ribs and low, slender spiral cords forming elongate beads at their intersection; aperture ovately lunate with six apertural barriers: three parietal lamellae expanded posteriorly with two long protruding beyond the aperture and one short and reset, two palatal nodules and one basal nodule; umbilicus wide, cup-shaped, diameter 0.66-0.82 mm (mean 0.78 mm) D/U 2.10-2.67 mm (mean 2.25 mm). Based on 21 measured specimens (QMMO86610 [10], QMMO86614 [10], QMMO86600 [1]).

Distribution and habitat. Carnarvon NP; living among rocks in vine thicket on basalt.

Remarks. *Rhophodon moffatt* sp. nov. is readily distinguished from the other charopids described here by the combination of tiny, discoidal shell with radially sculptured protoconch, wide cup-shaped umbilicus and the presence of six apertural barriers. *R. moffatt* most closely resembles the smaller *R. minutissimus* Stanisic, 1990 from SEQ in both general shell sculpture and the number of apertural barriers present. However, the latter differs in having three palatal barriers (rather than two) and in lacking a basal barrier.

Tristanoropa Holcroft, 2018

Tristanoropa Holcroft, 2018c: 98; Holcroft & Stanisic, 2018: 172.

Type species. *Tristanoropa hughesae* Holcroft, 2018- by original designation.

Diagnosis. Shell tiny, brown to golden-brown, discoidal, multi-whorled with a slightly sunken to slightly elevated spire, whorls numerous (>4.5) and tightly coiled; protoconch finely cancellate with 15-19 scalloped spiral cords and weak to prominent radial ribs, teleoconch with

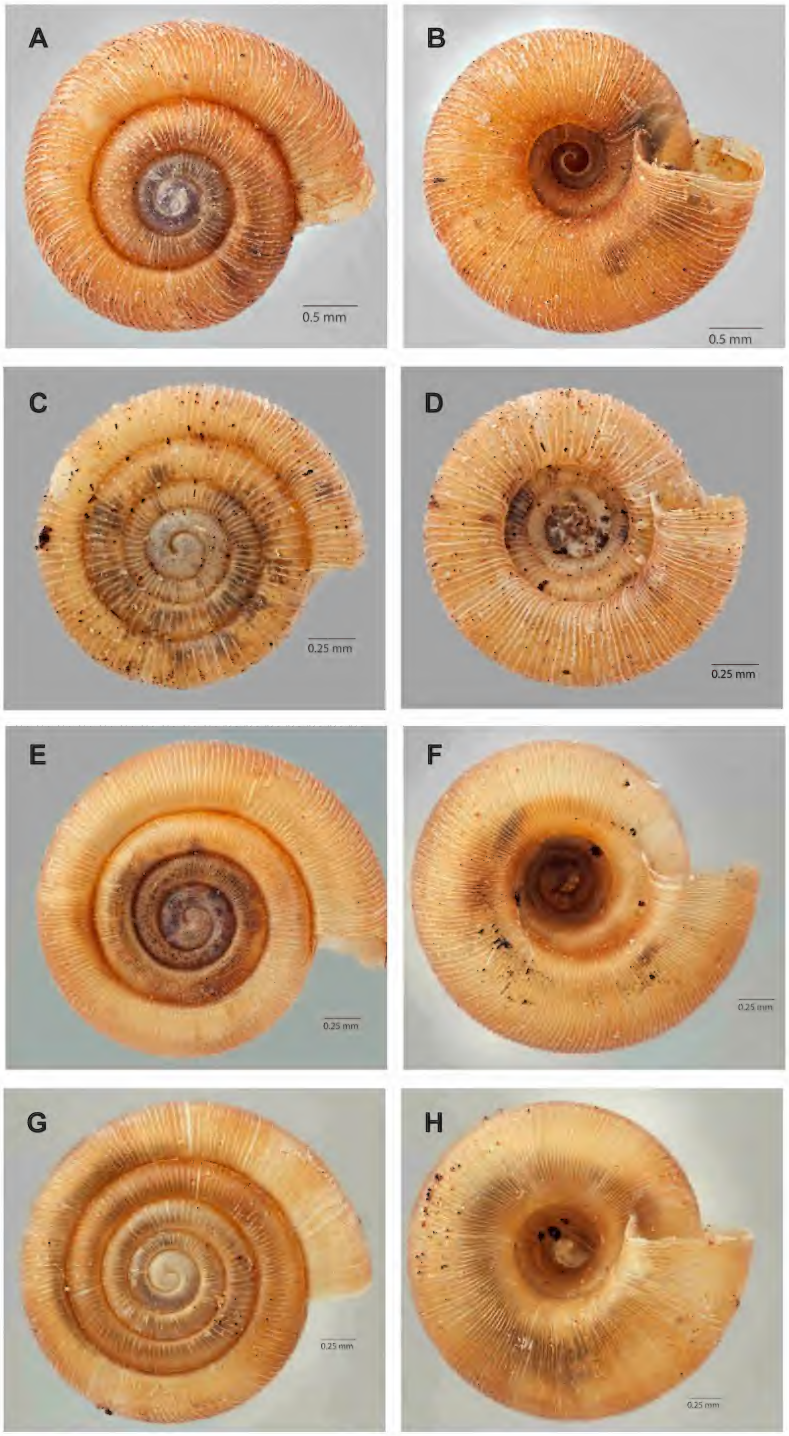

FIG. 1. Holotypes. **A-B**, *Spiraliropa carnarvon* Stanisic, 2010, QMMO66493; **C-D**, *Rhophodon moffatt* sp. nov., QMMO86600; **E-F**, *Tristanoropa saddler* sp. nov., QMMO86779; **G-H**, *T. crowman* sp. nov., QMMO86778,

crowded radial ribs; umbilicus wide V-shaped. Apertural barriers may or may not be present.

Remarks. *Tristanoropa* Holcroft, 2018 was introduced for MEQ charopids with 4.5 or more tightly coiled whorls, wide umbilicus and a finely cancellate protoconch consisting of scalloped spiral cords and prominent radial ribbing in a web-like arrangement (Holcroft 2018c). Holcroft and Stanisic (2018) added an additional four species from MEQ one of which (*Tristanoropa jaxut*) had weak rather than prominent radial ribs on the teleoconch. This trend is seen in two of the three species described below and has resulted in a slight modification of the generic diagnosis. The species described below are the first records of the genus from SCQ. Their localised distributions suggest that more species will be discovered in the numerous scattered vine thickets of the brigalow country.

Tristanoropa saddler sp. nov.
(Figs 1E–F, 6E)

Etymology. Named for Saddler Springs Station.

Preferred common name. Saddler Springs Pinwheel Snail.

Material examined. Holotype. QMMO86779, RC, Saddler Springs Stn, Carnarvon Range, SCQ, 25° 04′ 48″ S, 148° 07′ 27″ E, vine thicket on basalt scree, among rocks, coll. C. Eddie, 11.xii.2008. Height of shell 1.23 mm, diameter 2.46 mm, width of umbilicus 0.98 mm, D/U 2.50, H/D 0.50, whorls 4.625.

Paratypes. QMMO79445, 4RC; QMMO86607, 10RC, same data as holotype.

Diagnosis. Shell tiny, with a flat to slightly sunken spire, whorls tightly coiled; protoconch finely cancellate of 1.625 whorls with spirals and radials forming a web-like pattern, teleoconch with very crowded radial ribs (mean 98 on first whorl); umbilicus wide V-shaped. Apertural barriers absent.

Description. Shell tiny, golden-brown, discoidal with flat to slightly sunken spire; whorls 4.50-4.625, tightly coiled, sutures impressed; diameter 2.38-2.46 mm (mean 2.42 mm), height 1.23 mm, H/D 0.50-0.52 (mean 0.51); protoconch finely cancellate of 1.625 whorls, diameter 410 μm, sculptured with 17-19 scalloped spiral cords and prominent radial ribs forming a web-like pattern; teleoconch sculpture of bladed, crowded radial ribs 97-98 (mean 98) on the first whorl, microsculpture of weak microradial threads and crowded, prominent microspiral cords forming elongate beads at their intersection; umbilicus wide V-shaped, diameter 0.98-1.07 mm (mean 1.02 mm), D/U 2.23-2.50 (mean 2.36). Based on 2 measured specimens (QMMO86779, QMMO86607[1]).

Distribution and habitat. Known only from the type locality; living among rocks in vine thicket on basalt scree.

Remarks. *Tristanoropa saddler* sp nov. is micro-sympatric with *Rhophodon moffatt* sp. nov. but can be readily distinguished from that species by having a larger shell with greater number of whorls and lack of apertural barriers. The radial ribs on the protoconch of *T. saddler* are more pronounced than in the other two species described below.

Tristanoropa crowman sp. nov.
(Figs 1G-H, 6F-G)

Etymology. Named for Crowman Station.

Preferred common name. Crowman Pinwheel Snail.

Material examined. All SCQ. Holotype. QMMO86778, RC, Injune, 31 km WNW at Crowman Stn, N slope of Mt Hutton, 25° 49′ 29″ S, 148° 15′ 24″ E, sevt on basalt scree, undersides of rocks, coll. C. Eddie, B. Cosh, 2.xi.2017. Height of shell 1.48 mm, diameter 2.70 mm, width of umbilicus 1.07 mm, D/U 2.54, H/D 0.55, whorls 5.00.

Paratypes. QMMO86585, 3SC/13RC, same data as holotype.

Other material. QMMO66516, 3SC/10RC, Injune, WNW at Oakwells Stn, 25° 48′ 05″ S, 148° 15′ 14″ E, sevt on basalt scree, under rocks, coll. C. Eddie, 10.vi.1999.

Diagnosis. Shell tiny, with a flat to slightly elevated spire, whorls tightly coiled; protoconch finely cancellate of 1.5 whorls with crisp spirals over weaker radial ribs, teleoconch with crowded radial ribs (mean 59 on first whorl); umbilicus wide V-shaped. Apertural barriers absent.

Description. Shell tiny, golden-brown, discoidal with slightly sunken spire; whorls

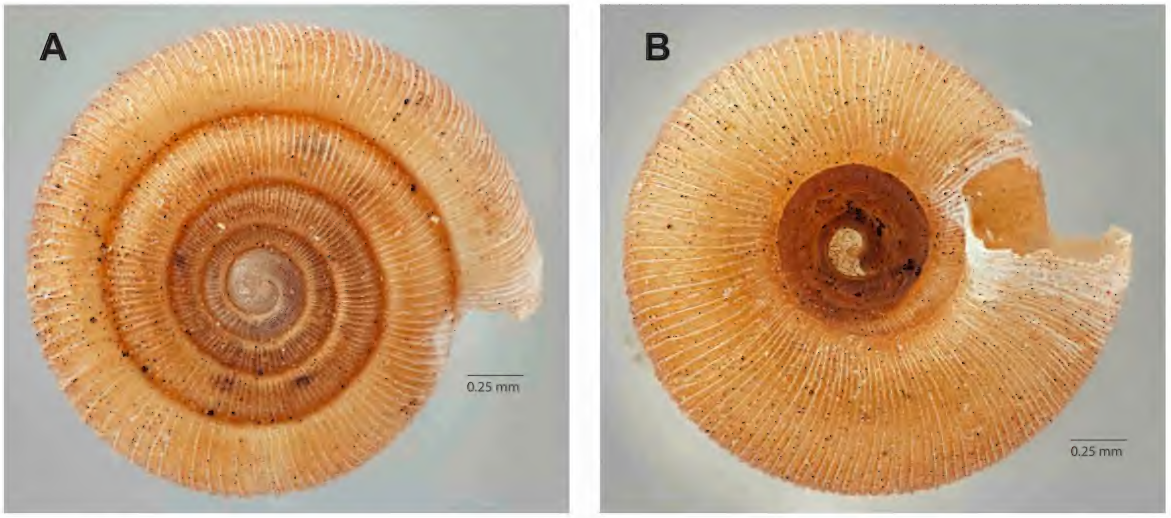

FIG. 2. **A-B**, *Tristanoropa palmgrove* sp. nov., QMMO86780, holotype.

FIG. 3. **A-B**, *Brigaloropa costulata* sp. nov., QMMO86781, holotype.

4.75-5.00, tightly coiled, sutures impressed; diameter 2.30-2.70 mm (mean 2.54 mm), height 1.23-1.48 mm (mean 1.36 mm), H/D 0.52-0.55 (mean 0.54); protoconch finely cancellate of 1.5 whorls, diameter 410 µm, sculptured with 15-17 scalloped spiral cords and weak radial ribs; teleoconch sculpture of bladed, crowded radial ribs 48-71 (mean 59) on the first whorl, microsculpture of weak microradial threads and low, weak microspiral cords forming weak elongate beads at their intersection; umbilicus wide V-shaped, diameter 1.07-1.15 mm (mean 1.10 mm), D/U 2.15-2.54 (mean 2.31). Based on 5 measured specimens (QMMO86778, QMMO86585[4]).

Distribution and habitat. Known only from Crowman and Oakwells Stns, SCQ; living on the underside of rocks in vine thicket on basalt scree.

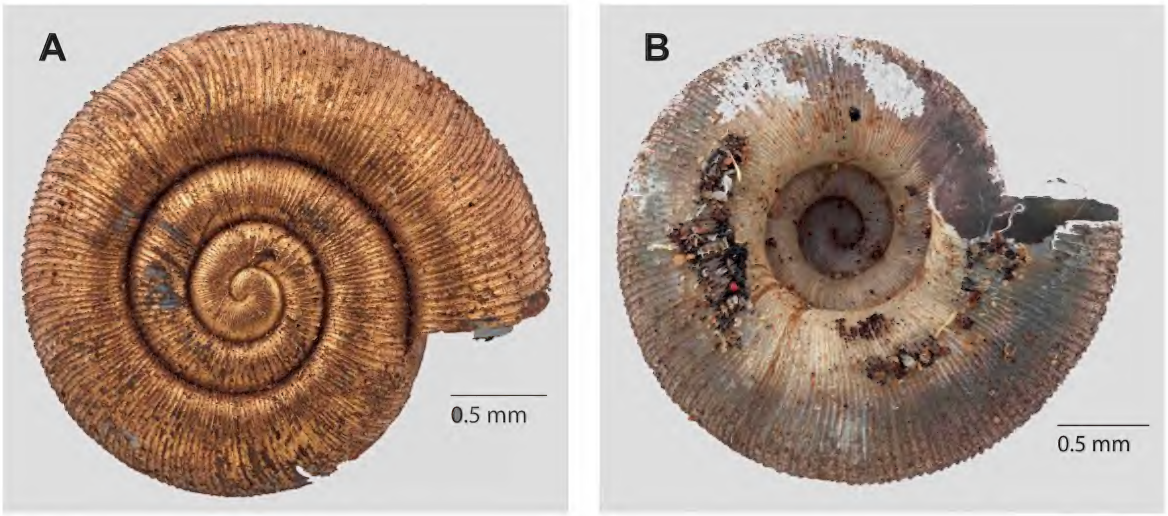

FIG. 4. **A-B**, *Arcadiaropa sunnyholt* sp. nov., QMMO79452, holotype.

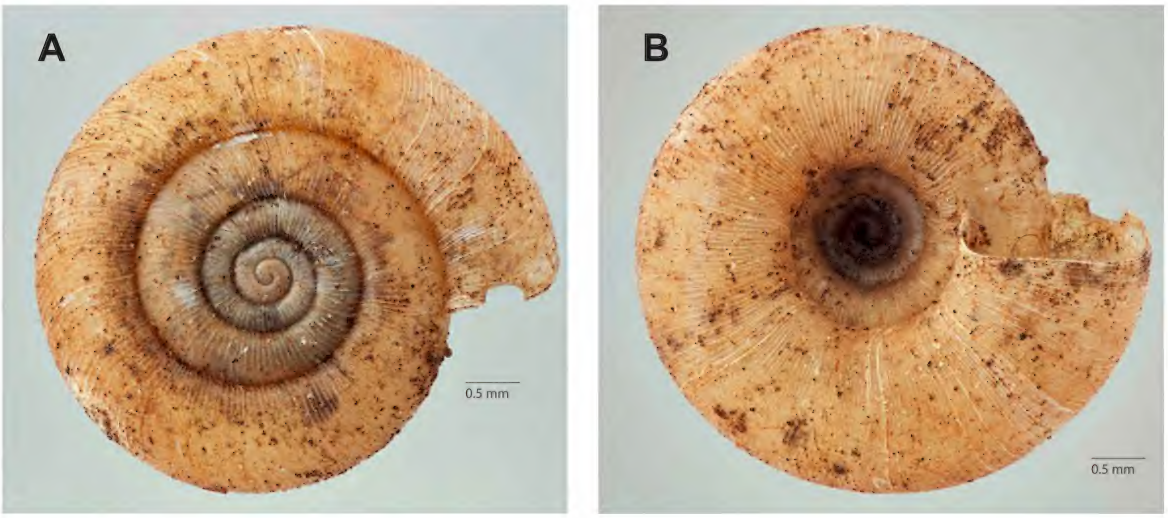

FIG. 5. **A-B**, *Eddiea carnarvon* sp. nov., QMMO86789, holotype.

Remarks. *Tristanoropa crowman* sp. nov. differs from *T. saddler* sp. nov. by having a greater number of whorls, weaker protoconch ribbing and less crowded teleoconch ribbing.

Tristanoropa palmgrove sp. nov.
(Figs 2A-B, 6H, 7A-B, 8)

Etymology. Named for Palmgrove National Park.

Preferred common name. Palmgrove Pinwheel Snail.

Material examined. Holotype. QMMO86780, RC, Palmgrove NP (Scientific), Bigge Range, SCQ, 25° 58′ 42″ S, 149° 24′ 53″ E, sevt in gorge with boulders, in leaf litter among logs/rocks, coll. C. Eddie, F. Carter, 28.ix.2001. Height of shell 1.23 mm, diameter 2.38 mm, width of umbilicus 0.98 mm, D/U 2.42, H/D 0.52, whorls 5.125.

Paratypes. QMMO86624, 45RC, same data as holotype; QMMO86621, 51RC, Palmgrove NP (Scientific), Middle Creek, SCQ, 25° 58′ 59.5″ S, 149° 13′ 32″ E, sevt on hill slope above watercourse, in leaf litter

under logs and bark piles at the base of trees, coll. C. Eddie, 13.xii.2000.

Other material. QMMO86618, 31RC, Palmgrove NP (Scientific), Middle Bigge Range, SCQ, 25° 58′ 59″ S, 149° 13′ 30″ E, sevt on slope beside watercourse, in leaf litter among logs/rocks, coll. C. Eddie, 14.xii.2000; QMMO73323, 45RC, Palmgrove NP, on E side of un-named hills, SCQ, 25° 01′ 47″ S, 149° 14′ 55″ E, sevt, in litter, coll. C. Eddie, 26.ix.2001.

Diagnosis. Shell tiny, with a flat to slightly sunken spire, whorls tightly coiled; protoconch finely cancellate of 1.5 whorls with crisp spirals over much weaker radial ribs, teleoconch with crowded radial ribs (mean 89 on first whorl); apertural barriers present in sub-adult specimens; umbilicus very wide V-shaped.

Description. Shell tiny, golden-brown, discoidal with slightly sunken spire; whorls 4.875-5.250, tightly coiled, sutures impressed; diameter 2.05-2.38 mm (mean 2.17 mm), height 0.98-1.31 mm (mean 1.12 mm), H/D 0.48-0.56 (mean 0.52); protoconch finely cancellate of 1.5 whorls, diameter 410 µm, sculptured with 15-17 scalloped spiral cords and weak radial ribs; teleoconch sculpture of bladed, crowded radial ribs 78-112 (mean 89) on the first whorl, microsculpture of weak microradial threads and weak microspiral cords forming weak elongate beads at their intersection; six apertural barriers present in sub-adult specimens (to about 4.5 whorls): three long palatal lamellae expanded posteriorly, two supra-palatal traces and one short basal lamellae; umbilicus very wide V-shaped, diameter 0.82-1.07 mm (mean 0.95 mm), D/U 1.69-2.55 (mean 2.30). Based on 17 measured specimens (QMMO86780, QMMO86624[4], QMMO86618[4], QMMO86621[3], QMMO73323[5]).

Distribution and habitat. Known only from Palmgrove NP, Bigge Range, SCQ; living in litter among logs and rocks in vine thicket.

Remarks. *Tristanoropa palmgrove* sp. nov. is distinguished from both *T. saddler* sp. nov. and *T. crowman* sp. nov. by the combination of very crowded ribs on the teleoconch and the possession of apertural barriers in sub-adult growth stages that are fully resorbed prior to becoming adult (Fig. 8). As far as is known this is the first record of total barrier resorption in any species of Charopidae. In Pacific Island and Australian charopids with barriers that have been studied to date, these appear shortly after hatching and are added to anteriorly and resorbed posteriorly through to adulthood (Solem 1983; Stanisic 1990). Barriers constrict the aperture and ostensibly protect the snail against prey such as ants. The question arises as to what function do the barriers in this species serve? Another intriguing aspect is the lack of any parietal barriers which are the most commonly encountered barriers in other charopids.

Brigaloropa gen. nov.

Type species. *Brigaloropa costulata* sp. nov. -herein designated.

Etymology. A contraction of brigalow combined with a contraction of Charopa.

Diagnosis. Shell tiny, white, subdiscoidal with a domed spire, whorls evenly coiled, sutures impressed; protoconch radial with widely spaced, bold radial ribs, teleoconch with bold, moderately spaced and curved radial ribs; umbilicus wide U-shaped.

Remarks. *Brigaloropa* gen. nov. can be distinguished by the following combination of characters: white shell, radial protoconch, dome-shaped spire, bold radial ribs on the teleoconch and wide U-shaped umbilicus.

Brigaloropa costulata sp. nov.
(Figs 3A-B, 7C-D)

Etymology. From the Latin *costulatus* = ribbed, referring to the pronounced, radially ribbed shell sculpture.

Preferred common name. Costulate Pinwheel Snail.

Material examined. Holotype. QMMO86781, RC, Palmgrove NP, on E side of un-named hills, SCQ, 25° 01′ 47″ S, 149° 14′ 55″ E, sevt, in litter, coll. C. Eddie, 26.ix.2001. Height of shell 1.23 mm, diameter 2.38 mm, width of umbilicus 0.82 mm, D/U 2.90, H/D 0.52, whorls 4.500.

Paratypes. QMMO73322, 22RC, same data as holotype.

Diagnosis. As for genus.

Description. Shell tiny, white, subdiscoidal with a domed spire; whorls 4.125-4.750, evenly coiled, sutures impressed; diameter 2.21-2.70

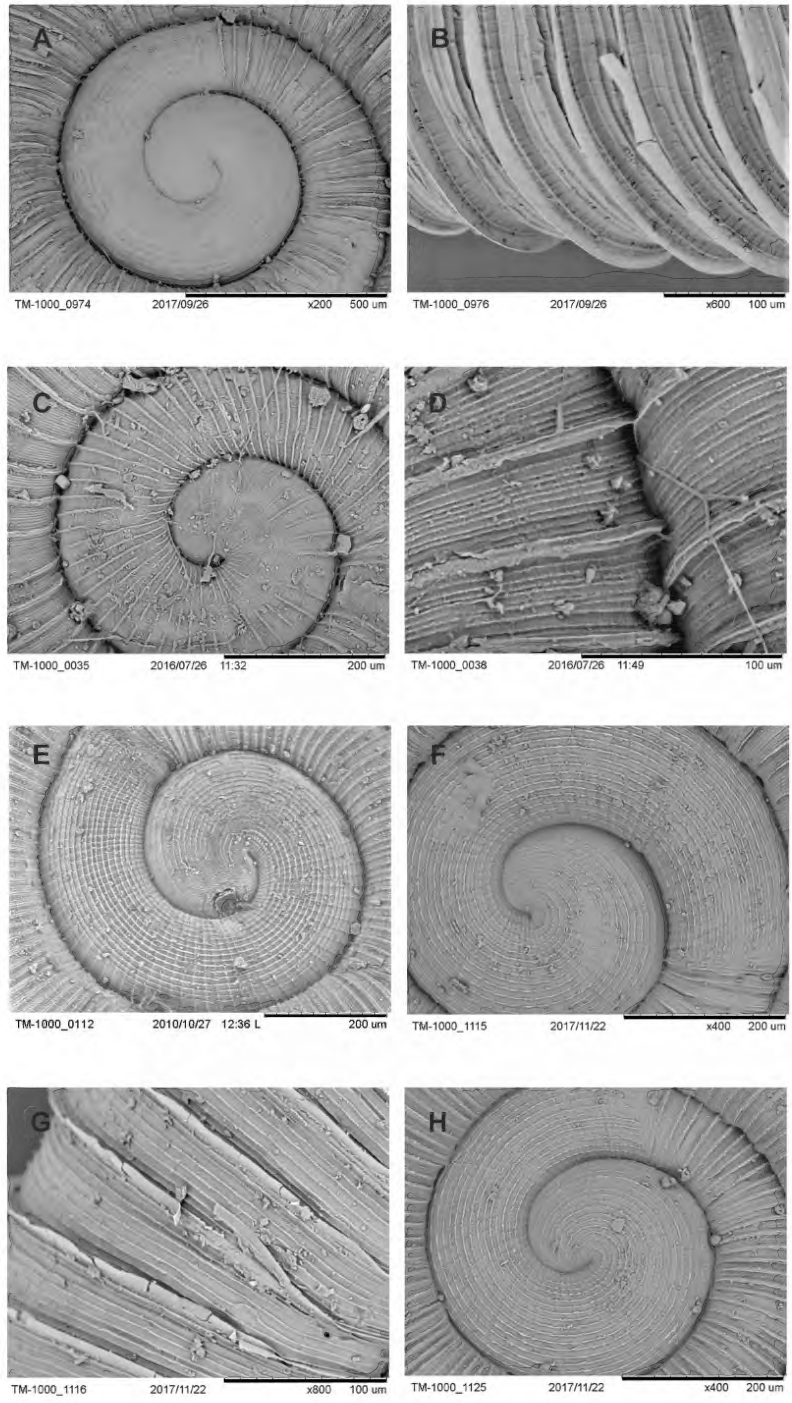

FIG. 6. Shell sculpture. **A-B**, *Spiraliropa carnarvon* Stanisic, 2010, QMMO78979. **A**, protoconch; **B**, teleoconch. **C-D**, *Rhophodon moffatt* sp. nov. , QMMO79444. **C**, protoconch; **D**, teleoconch. **E**, *Tristanoropa saddler* sp. nov., QMMO79445, protoconch; **F-G**, *T. crowman* sp. nov., QMMO66516. **F**, protoconch; **G**, teleoconch. **H**, *T. palmgrove* sp. nov., QMMO86624, protoconch.

mm (mean 2.39 mm), height 1.23-1.56 mm (mean 1.33 mm), H/D 0.52-0.60 (mean 0.56); protoconch radial of 1.75 whorls, diameter 410um, sculptured with bold, widely spaced radial ribs; teleoconch with moderately spaced curved, bold radial ribs 51-60 (mean 54) on the first whorl, microsculpture of fine interstitial radial threads and crowded microspiral cords forming bead-like nodules at their intersection; umbilicus very wide U-shaped, diameter 0.82-0.90 mm (mean 0.89 mm), D/U 2.45-2.90 (mean 2.68). Based on 11 measured specimens (QMMO86781, QMMO73322 [10]).

Distribution and habitat. Known only from Palmgrove NP, Bigge Range, SCQ; recovered from litter in vine thicket.

Remarks. *Brigaloropa costulata* sp. nov. is immediately recognizable by the tiny white shell with domed spire, prominent radial sculpture and wide U-shaped umbilicus. The minute and widespread *Discocharopa aperta* (Möllendorff, 1888) also has a white shell with flat spire, much more crowded radial ribs on the teleoconch and a very wide saucer-shaped umbilicus. *D. aperta* also lacks spiral microsculpture on the teleoconch.

Arcadiaropa gen. nov.

Type species. *Arcadiaropa sunnyholt* sp. nov.-herein designated.

Etymology. A combination of Arcadia and a contraction of Charopa.

Diagnosis. Shell tiny, light brown, discoidal, nautiliform with a slightly sunken spire; protoconch superior radial with prominent, slender and curved radial ribs and low spiral cords that become visible toward the protoconch-teleoconch boundary; teleoconch with very crowded, bladed radial ribs; umbilicus wide, U-shaped.

Remarks. *Arcadiaropa* gen. nov. is introduced to accommodate a nautiliform species with a superior radial protoconch in which weak spiral cords appear toward the protoconch-teleoconch boundary. In possessing continuous weak spiral cords, the superior radial protoconch differs from the strictly radial protoconchs seen in *Rhophodon* Hedley, 1924 and *Brigaloropa* gen. nov. Although appearing similar, the protoconch of *Arcadiaropa* differs from the early spiral protoconch of the MEQ *Radiolaropa* Holcroft, 2018 in lacking spiral elements on the first whorl.

Arcadiaropa sunnyholt sp. nov.
(Figs 4A-B, 7E-G)

Etymology. For Sunnyholt Station, Arcadia Valley, SCQ.

Preferred common name. Sunnyholt Pinwheel Snail

Material examined. Holotype. QMMO79452, RC, Sunnyholt Stn, Arcadia Valley, NE Injune, SCQ, 25° 17′ 14″ S, 148° 55′ 21″ E, sevt on sandstone slope, in litter among rocks, coll. C. Eddie, 01.x.2008. Height of shell 1.41 mm, diameter 2.60 mm, width of umbilicus 1.28 mm, D/U 2.03, H/D 0.52, whorls 3.750.

Diagnosis. Shell tiny, light brown, discoidal, nautiliform with a slightly sunken spire; sutures strongly impressed; protoconch superior radial with crowded, slender radial ribs and low spiral cords appearing toward the protoconch-teleoconch boundary; teleoconch with very crowded, bladed radial ribs (95 on the first whorl); umbilicus very wide, U-shaped.

Description. Shell tiny, light brown, discoidal, nautiliform with a slightly sunken spire; whorls 3.75, evenly coiled, rounded; sutures strongly impressed; diameter 2.60 mm, height 1.41 mm, H/D 0.54; protoconch superior radial, of 1.5 whorls, diameter 625 µm, sculptured with crowded, slender radial ribs and low spiral cords appearing toward the protoconch-teleoconch boundary; teleoconch with very crowded, bladed radial ribs, 95 on the first whorl (180 on last whorl); microsculpture of prominent microradial threads over very low microspiral cords forming weak buttresses at their intersection with the microradials; umbilicus very wide U-shaped, diameter 1.28 mm, D/U 2.03. Based on one measured specimen (QMMO79452).

Distribution and habitat. Known only from the type locality; recovered from litter in vine thicket on sandstone.

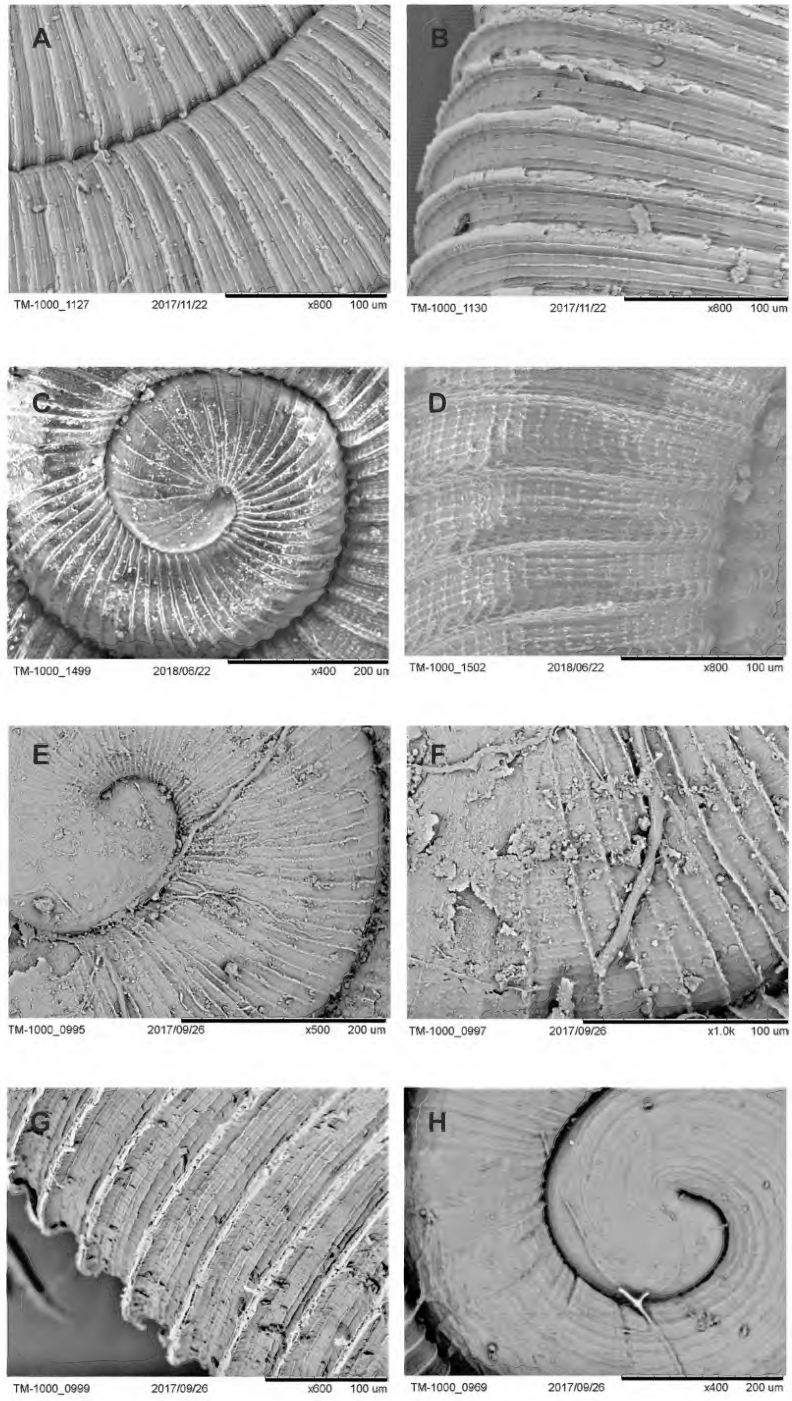

FIG. 7. Shell sculpture. **A-B**, *Tristanoropa palmgrove* sp. nov., QMMO86780. **A-B**, teleoconch; **C-D**, *Brigaloropa costulata* sp. nov., QMMO73322. **C**, protoconch; **D**, teleoconch. **E-G**, *Arcadiaropa sunnyholt* sp. nov., QMMO79452. **E**, protoconch; **F**, protoconch close-up showing spiral elements; **G** teleoconch. **H**, *Eddiea carnarvon* sp. nov., QMMO80259, protoconch.

Remarks. *Arcadiaropa sunnyholt* sp. nov. is known only from a single specimen but can be readily distinguished by the combination of nautiliform shell with superior radial protoconch, heavily ribbed teleoconch and very wide U-shaped umbilicus. The protoconch of *A. sunnyholt* bears some similarity to that of *Radiolaropa. danieli* Holcroft, 2018 but the two species differ in the intensity of the spiral cords on the protoconch. The illustrated type specimen is slightly sub-adult and gold coated for SEM.

Eddiea gen. nov.

Type species. *Eddiea carnarvon* sp nov.-herein designated.

Etymology. Named for Craig Eddie.

Diagnosis. Shell tiny, discoidal, nautiliform with a slightly sunken spire; protoconch superior spiral of 1.625 whorls with 12-17 broad, widely and regularly spaced rounded spiral cords and broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded radial ribs, umbilicus wide V to wide U-shaped.

Remarks. *Eddiea* gen. nov. is introduced to accommodate species with a superior spiral protoconch of 1.625 whorls on which radial ribs appear after 1.25 whorls. It differs from *Amfractaropa* Holcroft, 2018 (type *A. bretti* Holcroft, 2018) from the upland rainforests of the Clarke Range in MEQ which has a spiral protoconch of 1.75 whorls on which radial ribs appear after 1.50 whorls. The bimodal protoconch pattern (prominent broad spiral cords followed by prominent radial ribs on the last part of the protoconch) of *Eddiea* is also present in *Diphyoropa* Hyman & Stanisic, 2005 but the two genera differ in the structure of the spiral cords. Those of the species documented below are regularly spaced and of uniform height compared with those of *Diphyoropa* which are irregularly spaced and of irregular height.

Eddiea carnarvon sp. nov.
(Figs 5A-B, 7H, 11A)

Etymology. Named for Carnarvon Station Reserve.

Preferred common name. Carnarvon Station Pinwheel Snail.

Material examined. Holotype. QMMO86789, RC, Carnarvon Station, N of homestead, SCQ, 24° 47.935′ S, 147° 45.284′ E, sevt on basalt, in litter among rocks, coll. J. Stanisic, 11.x.2014. Height of shell 2.14 mm, diameter 4.74 mm, width of umbilicus 1.43 mm, D/U 3.31, H/D 0.45, whorls 4.875.

Paratypes. QMMO80249, 2SC/16RC, same data as holotype; QMMO80256, 2SC/27RC, Carnarvon Stn, N of homestead, SCQ, 24° 47.935′ S, 147° 45.284′ E, sevt on basalt, in litter among rocks, coll. J. Stanisic, 12.x.2014; QMMO80259, 28RC, Carnarvon Stn, N of homestead, SCQ, 24° 47.935′ S, 147° 45.284′ E, sevt on basalt, in litter among rocks, coll. J. Stanisic, 13.x.2014.

Other material. QMMO80238, 2RC, Piebald Spring, Carnarvon Stn, SCQ, 24° 49.871′ S, 147° 44.487′ E, remnant vine thicket/rocky outcrop, in litter among rocks, coll. J. Stanisic, 10.x.2014; QMMO80246, 3RC, Hillock N homestead, Carnarvon Stn, SCQ, 24° 48.627′ S, 147° 45.135′ E, vine thicket/basalt scree, in litter among rocks, coll. J. Stanisic, 11.x.2014.

Diagnosis. Shell tiny, brown, discoidal, nautiliform with a slightly sunken spire; protoconch superior spiral, of 1.625 whorls with broad, widely and regularly spaced rounded spiral cords initially and broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs (approx. 60 on the first whorl), umbilicus very wide U-shaped.

Description. Shell tiny, brown, discoidal, nautiliform with a slightly sunken spire; whorls 4.250-4.875 rounded, sutures strongly impressed; diameter 3.36-4.67 mm (mean 4.25 mm), height 1.72-2.46 mm (mean 2.07 mm), H/D 0.43-0.63 (mean 0.49); protoconch superior spiral, of 1.625 whorls, diameter 570 µm, sculptured with 12-15 broad, widely and regularly spaced rounded spiral cords initially, broad radial ridges only appearing after 1.25 whorls, forming nodules at their intersection; teleoconch with very crowded, bladed radial ribs (approx. 60 on the first whorl), microsculpture of microradial threads and low microspiral cords forming rounded beads at their intersection; aperture ovately lunate; umbilicus very wide U-shaped, diameter 1.48-2.13 mm (mean 1.81 mm), D/U 1.86-2.67 (mean 2.35). Based on 10 measured specimens (QMMO80259).

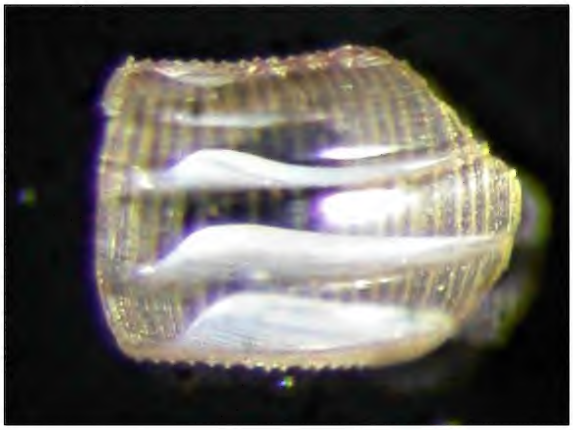

FIG. 8. Apertural barriers. Palatal barriers of *Tristanoropa palmgrove* sp. nov.

Distribution and habitat. Known only from Carnarvon Stn, SCQ; living under logs and rocks in vine thicket.

Remarks. *Eddiea carnarvon* sp nov. is confined to the vine thickets on Carnarvon Station, SCQ and occurs microsympatrically with the widespread *Spiraliropa carnarvon* Stanisic, 2010. *E. carnarvon* is distinguished from the latter by its larger size and by the broad, rounded spiral cords (approx. 15-17) and radial ribs on a slightly longer protoconch of 1.625 whorls. *S. carnarvon* has a strictly spiral protoconch of 1.5 whorls with 12-13 slender spiral cords.

Eddiea waddybrae sp. nov.
(Figs 9A-B, 11B-C)

Etymology. Named for Waddy Brae Station.

Preferred common name. Waddy Brae Pinwheel Snail.

Material examined. Holotype. QMMO86816, RC, Injune, 41.9 km ENE at Waddy Brae Station, SCQ, 28º 38′ 55.5″ S, 148º 55′ 39.7″ E, sevt on sandstone ridge, in leaf litter under/among rocks, coll. C. Eddie, H. Rose, 01.iv.2007. Height of shell 1.80 mm, diameter 3.69 mm, width of umbilicus 1.03 mm, D/U 2.65, H/D 0.49, whorls 4.375.

Paratypes. QMMO86578, 39RC, same data as holotype.

Other material. QMMO86579, 24RC, Injune, 51 km ENE at Fairview Station, SCQ, 25º 40′ 04″ S, 149º 02′ 24″ E, woodland with sevt understorey on sandstone ridge, in leaf litter around roots and boulders, coll. C. Eddie, A. Bendall, 18.xii.2013.

Diagnosis. Shell tiny, beige, discoidal, nautiliform with a flat spire; protoconch superior spiral, of 1.625 whorls with broad, widely and regularly spaced rounded spiral cords initially, broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs (approx. 75 on the first whorl), umbilicus very wide V-shaped.

Description. Shell tiny, light brown, discoidal, nautiliform with a flat spire; whorls 4.250-4.500 rounded, sutures strongly impressed; diameter 3.44-3.93 mm (mean 3.74 mm), height 1.72-2.05 mm (mean 1.84 mm), H/D 0.47-0.52 (mean 0.49); protoconch superior spiral, of 1.625 whorls, diameter 490 µm, sculptured with 15-17 broad, widely and regularly spaced, low rounded spiral cords initially, broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs 69-94 (mean 75) on the first whorl, microsculpture of microradial threads and low microspiral cords forming beads at their intersection; aperture ovately lunate; umbilicus very wide V-shaped, diameter 1.03-1.16 mm (mean 1.12 mm), D/U 3.34-3.36 (mean 3.35). Based on 10 measured specimens (QMMO86816, QMMO86578 [9]).

Distribution and habitat. Known only from the type locality and nearby Fairview Station, SCQ; living under rocks in vine thicket on sandstone.

Remarks. *Eddiea waddybrae* sp. nov. differs from *E. carnarvon* sp. nov. in having a smaller shell with less whorls and a smaller umbilicus. These two species are widely separated geographically with *E. waddybrae* occurring in a relatively drier environment on sandstone compared with the wetter basaltic environment of *E. carnarvon*. Specimens of *E. waddybrae* from the nearby Fairview Station have slightly coarser teleoconch sculpture but in all other aspects are similar to those from the type locality and are considered conspecific.

Eddiea oakwells sp. nov.
(Figs 9C-D, 11B-C)

Etymology. Named for Oakwells Station.

Preferred common name. Oakwells Pinwheel Snail.

Material examined. Holotype. QMMO86817, RC, Injune, WNW at Oakwells Station, SCQ, 25° 48′ 05″ S, 148° 15′ 14″ E, sevt on basalt scree, under rocks, coll. C. Eddie, 10.vi.1999. Height of shell 1.95 mm, diameter 3.90 mm, width of umbilicus 1.17 mm, H/D 0.50, D/U 3.33, whorls 4.375.

Paratypes. QMMO66515, 21RC, same data as holotype.

Diagnosis. Shell tiny, light brown, discoidal, nautiliform with a flat spire; protoconch superior spiral, of 1.625 whorls with broad, widely and regularly spaced rounded spiral cords initially and broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs (approx. 55-60 on the first whorl), umbilicus very wide U-shaped.

Description. Shell tiny, light brown, discoidal, nautiliform with a flat spire; whorls 4.375-4.625 rounded, sutures impressed; diameter 3.90-4.02 mm (mean 3.96 mm), height 1.95 mm, H/D 0.49-0.50 (mean 0.50); protoconch superior spiral, of 1.625 whorls, diameter 570 µm, sculptured with 15-17 broad, widely and regularly spaced, low rounded spiral cords initially, broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs 55-60 (mean 57) on the first whorl, microsculpture of microradial threads and low microspiral cords forming beads at their intersection; aperture ovately lunate; umbilicus very wide U-shaped, diameter 1.17 mm, D/U 3.33-3.44 (mean 3.38). Based on 2 measured specimens (QMMO86817, QMMO66515).

Distribution and habitat. Known only from the type locality; living under rocks in vine thicket on basalt scree.

Remarks. *Eddiea oakwells* sp. nov. has a slightly larger adult shell than *E. waddybrae* sp. nov. but smaller than that of *E. carnarvon* sp. nov.. *E. oakwells* can be further distinguished from the similar looking *E. waddybrae* by having more widely spaced ribs on the first teleoconch whorl and a slightly wider U-shaped rather than V-shaped umbilicus. The paratype series, while numerically sizeable, consists chiefly of juvenile and subadult specimens highlighting the general difficulty in collecting good adult series of charopids for study.

Eddiea bigge sp. nov.
(Figs9E-F, 11D-E)

Etymology. Named for the Bigge Range, SCQ.

Preferred common name. Bigge Range Pinwheel Snail.

Material examined. Holotype. QMMO86823, RC, Palmgrove NP (Scientific), Bigge Range, SCQ, 24° 58′ 42″ S, 149° 24′ 53″ E, sevt in narrow gorge with boulders, in litter under rocks/logs, coll. C. Eddie, F. Carter, 28.ix.2001. Height of shell 1.75 mm, diameter 3.57 mm, width of umbilicus 1.17 mm, H/D 0.49, D/U 3.06, whorls 4.375.

Paratypes. QMMO86619, 31RC, Palmgrove NP (Scientific), Middle Creek, SCQ, 24° 58′ 59″ S, 149° 13′ 30″ E, sevt on slope beside watercourse. Sandstone boulders/rocks, in litte runder rocks/logs, coll. C. Eddie, 14.xii.2000.

Other material. QMMO86622, 6RC, Palmgrove NP (Scientific), Middle Creek, SCQ, 24° 58′ 59″ S, 149° 13′ 32″ E, sevt on slope above watercourse/sandstone boulders and rocks, in litter under rocks/logs, coll. C. Eddie, 13.xii.2000; QMMO73324, 3RC, Palmgrove NP, on E side of unnamed hills, SCQ, 25° 01′ 47″ S, 149° 14′ 55″ E, sevt, coll. C. Eddie, 26.ix.2001.

Diagnosis. Shell tiny, golden brown, discoidal, nautiliform with a flat to slightly sunken spire; protoconch superior spiral of 1.625 whorls with broad, widely and regularly spaced, low rounded spiral cords initially, broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs, mean 75 on the first whorl; umbilicus wide U-shaped.

Description. Shell tiny, light brown, discoidal, nautiliform with a sunken spire; whorls 4.000-4.375 rounded, sutures impressed; diameter 3.11-3.57 mm (mean 3.33 mm), height 1.48-1.75 mm (mean 1.59 mm), H/D 0.45-0.49 (mean 0.47); protoconch superior spiral, of 1.625 whorls, diameter 490 µm, sculptured with 15-17 broad, widely and regularly spaced, low rounded spiral cords initially, broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs 69-79 (mean 74) on the first whorl, microsculpture of microradial threads and low microspiral cords forming beads at their intersection; aperture ovately lunate; umbilicus very wide U-shaped,

diameter 1.17-1.39 mm (mean 1.30 mm), D/U 2.24-3.06 (mean 2.60). Based on 4 measured specimens (QMMO86823, QMMO86619 [3]).

Distribution and habitat. Known only from Palmgrove NP, Bigge Range, SCQ; living under logs and rocks.

Remarks. *Eddiea bigge* sp. nov. occurs microsympatrically with several other charopids including *Spiraliropa Carnarvon* Stanisic, 2010. From this species *E. bigge* may be distinguished by the larger sized shell, longer superior spiral protoconch (spiral in *S. carnarvon*) with broad and rounded rather than slender spiral cords, less impressed sutures and wider umbilicus.

Platyumbiropa gen. nov.

Type species. *Platyumbiropa tabor* sp nov.-herein designated.

Etymology. A combination of the Greek platys = wide, and contractions of umbilicus and *Charopa*; referring to the very wide V-shaped umbilicus of the species.

Diagnosis. Shell tiny, discoidal, nautiliform with a slightly sunken spire; protoconch superior spiral of 1.625 whorls with 12-17 crowded, broad and regularly spaced flattish spiral cords, broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded radial ribs, umbilicus very wide V-shaped.

Remarks. *Platyumbiropa* gen. nov. differs from *Eddiea* gen. nov. by the combination of low and crowded, broad spiral cords on the protoconch and wide umbilicus compared with the bolder and much more widely spaced protoconch spirals and narrower umbilicus of *Eddiea.*

Platyumbiropa tabor sp. nov.
(Figs 9G-H, 12A-B)

Etymology. Named for Mount Tabor.

Preferred common name. Mount Tabor Pinwheel Snail.

Material examined. Holotype. QMMO86825, RC, Augathella, NE at Mt Tabor Station, ESE of Urandoo, SCQ, 25° 11′ 45″ S, 147° 30′ 59″ E, vine thicket on steep basalt scree, in leaf litter among rocks, Coll. C. Eddie, R. Aisthorpe, 21.x.2015. height of shell 1.80 mm, diameter 3.93 mm, width of umbilicus 1.89 mm, H/D 0.46, D/U 2.09, whorls 4.875.

Paratypes. MO86629, 34RC, same data as holotype.

Diagnosis. Shell tiny, light brown, discoidal, nautiliform with a sunken spire; protoconch superior spiral of 1.625 whorls with crowded, low, broad flattish spiral cords initially, broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs, mean 62 on the first whorl; umbilicus very wide V-shaped.

Description. Shell tiny, light-brown, discoidal, nautiliform with a sunken spire; whorls 4.125-4.875, rounded, sutures impressed; diameter 3.28-3.93 mm (mean 3.63 mm), height 1.56-1.80 mm (mean 1.67 mm), H/D 0.43-0.50 (mean 0.46); protoconch superior spiral, of 1.625 whorls, diameter 490 μm, sculptured with low, broad flattish spiral cords and broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs 60-67 (mean 62) on the first whorl, microsculpture of microradial threads and low microspiral cords forming beads at their intersection; aperture ovately lunate; umbilicus wide U-shaped, diameter 1.48-1.97 mm (mean 1.64 mm), D/U 1.88-2.42 (mean 2.20). Based on 12 measured specimens (QMMO86629[11], QMMO86825).

Distribution and habitat. Known only from the type locality; living among rocks in vine thicket on basalt scree.

Remarks. *Platyumbiropa tabor* sp. nov. is similar in size and shape to *P. grafton* sp. nov. but differs by having a light brown shell, more intense spiral cords on the protoconch and slightly larger umbilicus.

Platyumbiropa grafton sp. nov.
(Figs 10A-B, 12C-D)

Etymology. Named for the Grafton Range, SCQ.

Preferred common name. Grafton Range Pinwheel Snail.

Material examined. Holotype. MO86824, RC, Grafton Range, NE Roma at Belbri Station, SCQ, 26° 25′ 15″ S, 148° 54′ 33″, vine thicket/open woodland, in litter, coll. C. Eddie, 13.xii.2001. Height of shell 1.72 mm,

diameter 4.10 mm, width of umbilicus 1.42 mm, H/D 0.42, D/U 2.89, whorls 4.750.

Paratypes. QMMO86573, 5RC, Grafton Range, NE Roma at Belbri Station, SCQ, 26° 24′ 44″ S, 148° 55′ 15″, sevt in gully/basalt, in leaf litter under logs and rocks, coll. C. Eddie, 13.xii.2001; QMMO87172, 24RC, Grafton Range, NE Roma, SCQ, 26° 24′ 12″ S, 148° 54′ 43″, vine thicket/figs/*Brachychiton*, in litter among rocks at base of fig, coll, C. Eddie, M, Gane, 13. xi.2016.

Other material. QMMO73115, 1RC, Grafton Range, NE Roma at Belbri Station, SCQ, 26° 25′ 15″ S, 148° 54′ 33″, vine thicket/open woodland, in litter, coll. C. Eddie, 13.xii.2001; QMMO86571, 1RC, Grafton Range, NE Roma at Belbri Station, SCQ, 26° 24′ 54″ S, 148° 55′ 18″, vine thicket/open forest, in litter under logs and fallen bark, coll. C. Eddie, 27.iv.2003; QMMO86572, 3RC, Grafton Range, NE Roma at Belbri Station, SCQ, 26° 24′ 54″ S, 148° 55′ 04″, sevt/basalt, in litter under logs/rocks, coll. C. Eddie, 14.iv.2008.

Diagnosis. Shell tiny, golden brown, discoidal, nautiliform with a flat to slightly sunken spire; protoconch superior spiral of 1.625 whorls with barely visible, low, broad, flattish spiral cords initially, broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs, mean 60 on the first whorl; umbilicus very wide V-shaped.

Description. Shell tiny, golden brown, discoidal, nautiliform with a sunken spire; whorls 4.125-4.750, rounded, sutures impressed; diameter 3.28-4.10 mm (mean 3.64 mm), height 1.56-1.72 mm (mean 1.66 mm), H/D 0.42-0.48 (mean 0.46); protoconch superior spiral, of 1.625 whorls, diameter 490 μm, sculptured with barely visible low, broad, flattish spiral cords, broad radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs 60-61 (mean 61) on the first whorl, microsculpture of microradial threads and low microspiral cords forming beads at their intersection; aperture ovately lunate; umbilicus wide U-shaped, diameter 1.39-1.42 mm (mean 1.41 mm), D/U 2.89. Based on 2 measured specimens (QMMO86824, QMMO73115).

Distribution and habitat. Known only from Belbri Station, Grafton Range, SCQ; found in litter under logs and rocks in vine thicket.

Remarks. *Platyumbiropa grafton* sp. nov. differs from *P. tabor* sp. nov. chiefly by the very weak apical sculpture which is barely visible by both optical and scanning microscopy. *P. grafton* also has a smaller umbilicus than *P. tabor*. Much of the Grafton Range has been cleared for farming and the few remaining bottle trees indicate the past presence of more extensive vine thicket communities in the area.

Carnaropa gen. nov

Type species. *Carnaropa racecourse* sp nov.-herein designated.

Etymology. A combination of a contraction of Carnarvon and a contraction of Charopa.

Diagnosis. Shell tiny, discoidal, nautiliform with a slightly sunken spire; protoconch superior spiral of 1.625 whorls with 9-11 widely and regularly spaced, wide and flat spiral cords and slender radial ribs only appearing after 1.25 whorls; teleoconch with very crowded radial ribs, umbilicus wide V to wide U-shaped.

Remarks. *Carnaropa* gen. nov. differs from *Eddiea* in having slender and widely spaced spiral cords on protoconch as opposed to the crowded, and relatively broad spiral cords of the latter. Currently the genus is only known from two species in two locations in the Carnarvon NP, SCQ. However, given the difficulty in collecting these tiny snails, additional species may yet be found in other locations within the Carnarvon Range.

Carnaropa racecourse sp. nov.
(Figs 10C-D, 12E-F)

Etymology. Named for Racecourse Spring, Mt Moffatt Section, Carnarvon NP, SCQ.

Preferred common name. Racecourse Spring Pinwheel Snail

Material examined. Holotype. QMMO86820, RC, Carnarvon NP, Mt Moffatt Section, ridge NW Lots Wife, SCQ, 24° 56′ 00″ S, 148° 05′ 43″ E, sevt/sandstone, in litter, coll. C. Eddie, 22.i.1999. Height of shell 2.01 mm, diameter 3.90 mm, width of umbilicus 1.30 mm, H/D 0.52, D/U 3.00, whorls 4.500.

Paratypes. QMMO86602, 23RC, same data as holotype.

Other material. QMMO86599, 1RC, Carnarvon NP, Mt Moffatt Section, gorge downstream of Racecourse Spring, SCQ, 24° 56′ 04″ S, 148° 05′ 49″ E, basalt scree with vines, in leaf litter among rocks, coll. C. Eddie, 18.ii.2002; QMMO66459, 1RC, Carnarvon NP, Mt Moffatt Section, at Racecourse Spring, SCQ, 24° 56′ 00″ S, 148° 05′ 43″ E, coll. C. Eddie, 22.i.1999.

Diagnosis. Shell tiny, golden brown, discoidal, nautiliform with a flat to slightly sunken spire; protoconch superior spiral of 1.625 whorls with 9-11 widely and regularly spaced, wide and flat spiral cords, slender radial ribs only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs, mean 80 on the first whorl; umbilicus wide U-shaped.

Description. Shell tiny, golden brown, discoidal, nautiliform with a slightly sunken spire; whorls 4.125-4.625, rounded, sutures impressed; diameter 3.70-3.90 mm (mean 3.78 mm), height 1.68-2.01 mm (mean 1.84 mm), H/D 0.45-0.52 (mean 0.49); protoconch superior spiral, of 1.625 whorls, diameter 490 µm, sculptured with 9-11 widely and regularly spaced, wide and flat spiral cords, slender radial ribs only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs 76-85 (mean 80) on the first whorl, microsculpture of microradial threads and low microspiral cords forming beads at their intersection; aperture ovately lunate; umbilicus wide U-shaped, diameter 1.10-1.30 mm (mean 1.24 mm), D/U 2.74-3.36 (mean 3.01). Based on 5 measured specimens (QMMO86820, QMMO86602 [4]).

Distribution and habitat. Mt Moffatt Section, Carnarvon NP, SCQ; living under rocks in vine thicket.

Remarks. *Carnaropa racecourse* sp. nov. is distinguished from the geographically proximate *Eddiea carnarvon* sp. nov. by a combination of smaller shell with fewer and more slender apical spiral cords, a greater number of ribs on the first whorl and narrower U-shaped umbilicus.

Carnaropa salvatorosa sp. nov.
(Figs 10E-F, 12G-H)

Etymology. Named for the Salvator Rosa Section, Carnarvon NP, SCQ.

Preferred common name. Salvator Rosa Pinwheel Snail.

Material examined. Holotype. AMSC162130, RC, Belinda Springs, Salvator Rosa Section, Carnarvon Gorge NP, SCQ, 24° 50.000′ S, 147° 11.750′ E, in litter from damp sides of spring outflow, coll. W. F. Ponder, P. H. Colman, 29.ix.1984. Height of shell 1.72 mm, diameter 3.44 mm, width of umbilicus 1.23 mm, H/D 0.50, D/U 2.80, whorls 4.5.

Paratype. AMSC575657, 1RC, same data as holotype.

Diagnosis. Shell tiny, golden brown, discoidal, nautiliform with a slightly sunken spire; protoconch superior spiral of 1.625 whorls with 9-11 widely and regularly spaced, wide and flat spiral cords initially, slender radial ribs only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs, mean 70 on the first whorl; umbilicus wide U-shaped.

Description. Shell tiny, golden brown, discoidal, nautiliform with a slightly sunken spire; whorls 4.00-4.50, rounded, sutures impressed; diameter 3.20-3.44 mm (mean 3.32 mm), height 1.64-1.72 mm (mean 1.68 mm), H/D 0.50-0.51 (mean 0.51); protoconch superior spiral, of 1.625 whorls, diameter 410 µm, sculptured with 9-11 widely and regularly spaced, wide and flat spiral cords, slender radial ridges only appearing after 1.25 whorls; teleoconch with very crowded, bladed radial ribs 66-74 (mean 70) on the first whorl, microsculpture of microradial threads and low microspiral cords forming tiny beads at their intersection; aperture ovately lunate; umbilicus wide U-shaped, diameter 1.15-1.23 mm (mean 1.19 mm), D/U 2.79-2.80 (mean 2.79). Based on 2 measured specimens (AMSC162130, AMSC575657).

Distribution and habitat. Known only from the type locality; found in litter in damp places.

Remarks. *Carnaropa salvatorosa* sp. nov. differs from *Ca. racecourse* by the combination of smaller shell with smaller diameter protoconch, fewer ribs on the first whorl and less crowded ribs on the teleoconch. *Ca. salvatorosa* is the first charopid recorded from the western-most section of Carnarvon NP. Both *Ca. salvatorosa* and *Ca. racecourse* sp. nov. were found in

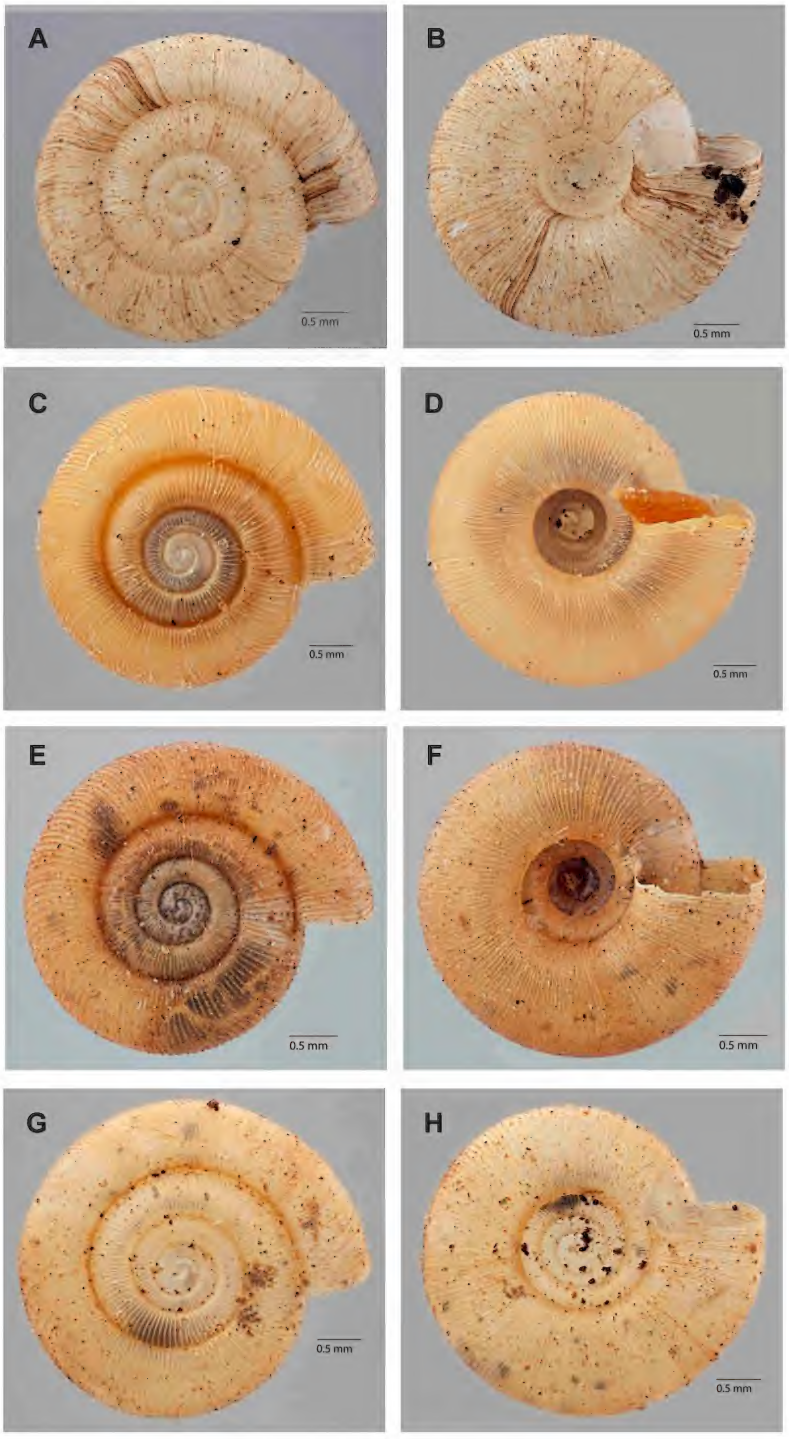

FIG. 9. Holotypes. **A-B**, *Eddiea waddybrae* sp. nov., QMMO86816; **C-D**, *E. oakwells* sp. nov., QMMO86817; **E-F**, *E. bigge* sp.nov., QMMO86823; **G-H**, *Platyumbiropa tabor* sp. nov., QMMO86825.

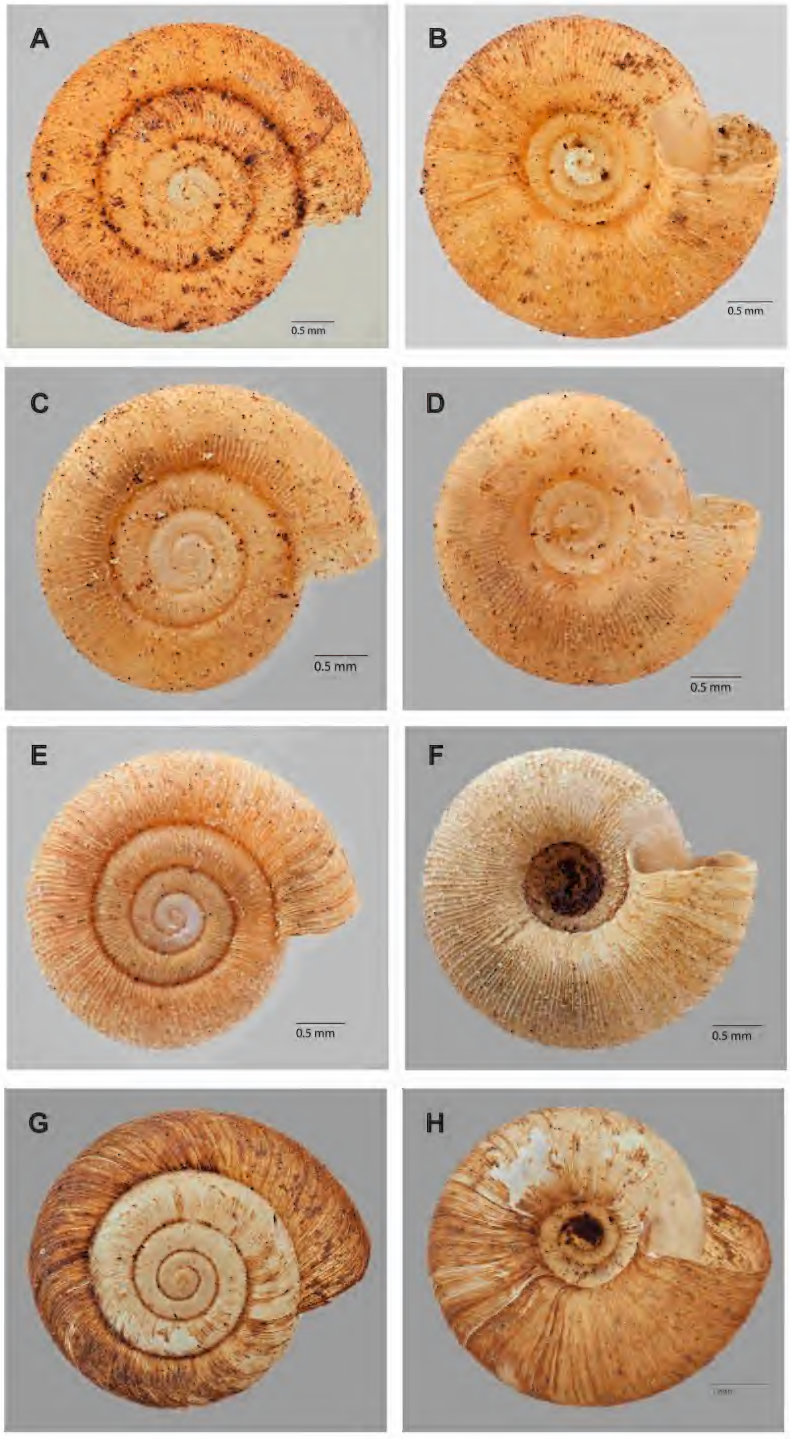

FIG. 10. Holotypes. **A-B**, *Platyumbiropa grafton* sp. nov., QMMO86824; **C-D**, *Carnaropa racecourse* sp. nov., QMMO86820; **E-F**,*Carnaropa salvatorosa* sp. nov., AMSC162130; **G-H**, *Cineropa roma* sp. nov., QMMO86826.

relatively damp places in otherwise drier eucalypt/*Callitris* forest.

Cineropa gen. nov.

Type species. *Cineropa roma* sp. nov.- herein designated.

Etymology. A contraction of the Latin *cinereus* = ash-colored alluding to the grey-brown shell colour, combined with a contraction of Charopa.

Diagnosis. Shell tiny, greyish-brown with darker periostracal streaks, discoidal with a flat to raised spire; protoconch superior spiral of 1.5 whorls with 25-35 crowded, slender and wrinkled, spiral cords overlying weak, low radial ridges that become more prominent on the latter part of the protoconch; teleoconch with very crowded, prominent, bladed radial ribs, umbilicus wide U-shaped.

Remarks. *Elsothera* Iredale, 1933 (type species. *Helix sericatula* Pfeiffer, 1849), as defined by Iredale (1937) and more recently Stanisic *et al*. (2010), is considered to be polyphyletic. *Tasmathera* Bonham (in Stanisic *et al*. 2018) and *Huntiana* Stanisic, 2018 (in Stanisic *et al*. 2018) were introduced to accommodate several southern Australian species previously included in *Elsothera* on the basis of major differences in protoconch sculpture from that of the type. *Cineropa* gen. nov. represents a further subdivision. *Cineropa* has a superior spiral protoconch (many crowded spiral cords) with weak radial ridges mainly toward the latter part of the protoconch. *Elsothera s.s.* as defined by *E. sericatula* (Pfeiffer, 1849) has a superior radial protoconch with crowded, bold and complex radial ribs and weaker spiral elements (Fig. 13D). A thorough revision of *Elsothera s.l.* as it currently stands is proposed but is beyond the scope of the current study. Both *Cineropa roma* sp. nov. and *Ci. hewittorum* (Stanisic, 1996) comb. nov. appear to prefer open woodland in contrast to many of the charopids included in this study that favour the moister and closed habitats provided by semi-evergreen vine thicket.

Cineropa roma sp. nov.
(Figs 10G-H, 13A-B)

Etymology. For the town of Roma, SCQ.

Preferred common name. Roma Pinwheel Snail.

Material examined. Holotype. QMMO86826, RC, Roma, NNW on Bungil Creek floodplain, SCQ, 26° 13′ 32″ S, 148° 42′ 00″E, cleared paddock/scattered trees, litter, coll. C. Eddie, 10.x.1999. Height of shell 3.11 mm, diameter 6.15 mm, width of umbilicus 1.89 mm, H/D 0.51, D/U 3.26, whorls 4.875.

Paratypes. QMMO66112, 9RC, same data as holotype.

Other material. QMMO86606, 1RC, Bungil Creek, 36 km NNW Roma, SCQ, 26° 15′ 18″ S, 148° 42′ 33″ E, eucalypt/*Casuarina* woodland, among soil on creek bank, coll. C. Eddie, 29.xi.2009.

Diagnosis. Shell tiny, greyish-brown with darker periostracal streaks, discoidal with a flat to raised spire; protoconch superior spiral of 1.5 whorls with numerous, crowded, regularly spaced, slender and wrinkled spiral cords overlying weak, low radial ridges that become more prominent on the latter part of the protoconch; teleoconch with very crowded, prominent, bladed radial ribs, umbilicus wide U-shaped.

Description. Shell tiny, greyish-brown, discoidal, with a flat to slightly raised spire; whorls 4.4.25-4.875, rounded, sutures impressed; diameter 5.25-6.15 mm (mean 5.56 mm), height 2.21-3.11 mm (mean 2.61 mm), H/D 0.42-0.55 (mean 0.47); protoconch superior spiral, of 1.5 whorls, diameter 690 µm, sculptured with 30-35 crowded, regularly spaced, wrinkled spiral cords overlying weak, low radial ridges that become more prominent on the latter part of the protoconch; teleoconch with very crowded, bladed radial ribs 42-59 (mean 52) on the first whorl, microsculpture of microradial threads and low microspiral cords forming tiny beads at their intersection; aperture ovately lunate; umbilicus wide U-shaped, diameter 1.89-2.21 mm (mean 2.05 mm), D/U 2.37-3.26 (mean 2.73). Based on 5 measured specimens (QMMO86826, QMMO66112[4]).

Distribution and habitat. Known only from the type locality; living in open woodland.

Remarks. *Cineropa roma* sp. nov. is the largest pinwheel snail yet recorded from the brigalow country. The species occupies a similar woodland habitat to that of *Ci. hewittorum* (Stanisic, 1996)

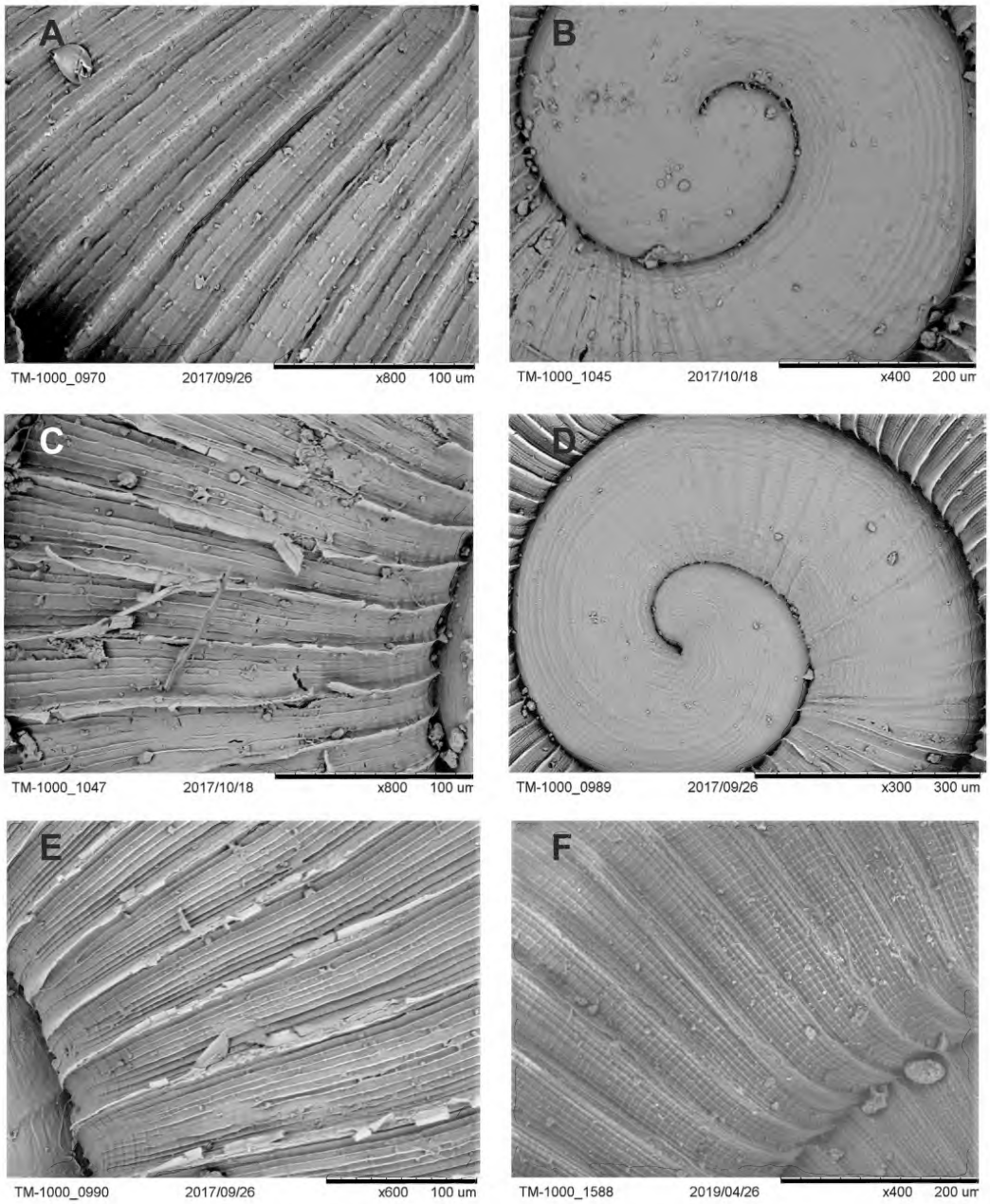

FIG. 11. Shell sculpture. **A**, *Eddiea carnarvon* sp. nov., QMMO80259, teleoconch; **B-C**, *E. waddybrae* sp. nov., QMMO86578. **B**, protoconch; **C**, teleoconch; **D-E**, *E. oakwells* sp. nov., QMMO66516. **D**, protoconch; **E**, teleoconch; **F**. *E. bigge* sp. nov., QMMO73324, teleoconch.

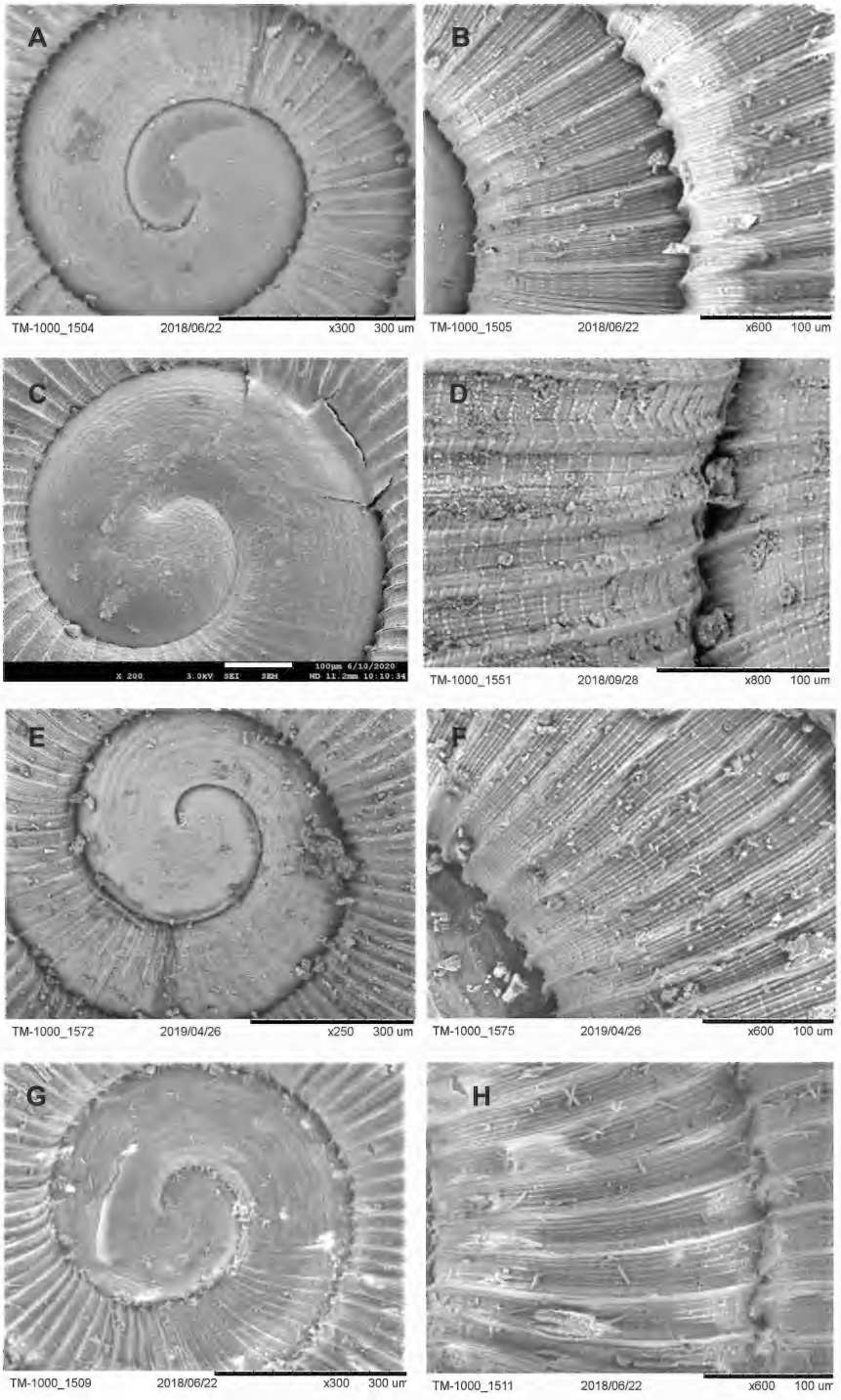

FIG. 12. Shell sculpture. **A-B**, *Platyumbiropa tabor* sp. nov., QMMO86629. **A**, protoconch; **B**, teleoconch. **C-D**, *P. grafton* sp. nov., **C**, QMMO87172, protoconch; **D**, QMMO86573, teleoconch. **E-F**, *Carnaropa racecourse* sp. nov., QMMO86602. **E**, protoconch; **F**, teleoconch. **G-H**, *Carnaropa salvatorosa* sp. nov., AMSC162130. **G**, protoconch; **H**, teleoconch.

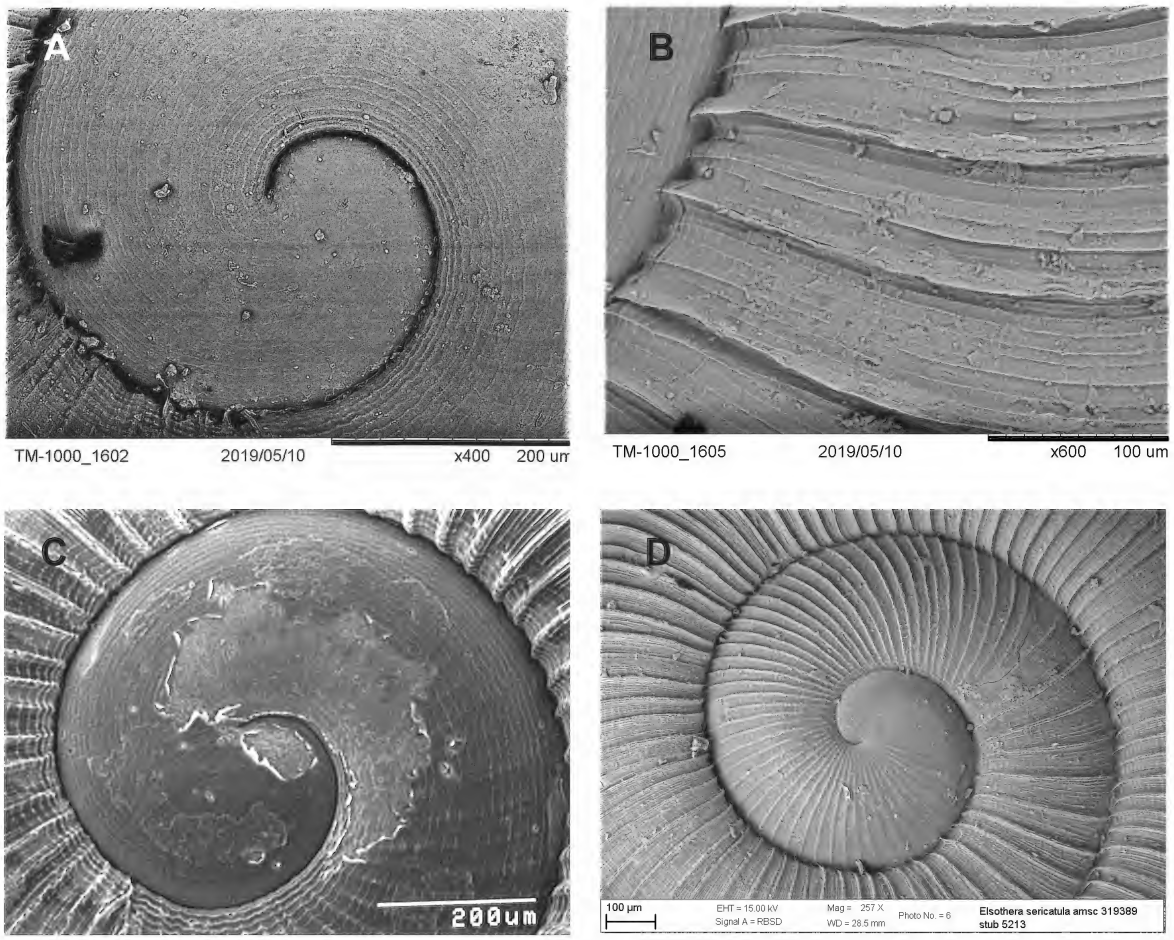

FIG. 13. Shell sculpture. **A-B**, *Cineropa roma* sp. nov., QMMO66112. **A**, protoconch; **B**, teleoconch. **C**, *Cineropa hewittorum* (Stanisic, 1996) comb. nov., QMMO56281, protoconch; **D**, *Elsothera sericatula* (Pfeiffer, 1849) AMSC319389, Concord, Sydney, NSW, teleoconch.

comb. nov. and is in contrast to the vine thicket habitats of other species included in this study.

Cineropa hewittorum (Stanisic, 1996) comb. nov. (Fig. 13C)

Common name. Dawson Valley Pinwheel Snail.

Diagnosis. Shell tiny, brown with darker periostracal streaks, discoidal with a flat to raised spire; protoconch superior spiral of 1.5 whorls with 28-30 crowded, regularly spaced, slender and wrinkled spiral cords overlying low, weak radial ridges that become more intense on the latter part of the protoconch; teleoconch with crowded, prominent, bladed radial ribs, umbilicus wide U-shaped.

Material examined. (Additional to Stanisic 1996). QMMO64384, 26SC/1RC, Theodore, S at Dawson River crossing on Isla-Delusion Rd, SEQ, 25° 11′ 01″ S, 150° 10′ 52″ E, palm/eucalypt, coll. J. Stanisic, G. Ingram, 20.viii.1997; QMMO60853,1SC/1RC, Dawson River crossing on Isla-Delusion Rd, SEQ, 25° 11′ 01″ S, 150° 10′ 52″ E, palm/eucalypt, coll. J. Stanisic, G. Ingram, 4.ii.1997; QMMO60807, 1RC, Taroom, E on Cracow Rd at Cockatoo Ck, SEQ, 25° 34′ 05″ S, 150° 05′ 08″, eucalypt woodland, under logs, coll. J Stanisic, 20.vi.1996; QMMO60746, 2RC, Taroom, ENE, along Dawson River near Nathan Gorge, SEQ, 25° 27′ 08″ S, 150° 08′ 12″ E, vine thicket/ eucalypt/palm, under logs, coll. J Stanisic, 14.vi.1996.

Remarks. Originally described from Mt Rose Stn, Taroom, SEQ and allocated to *Elsothera* Iredale, 1933 by Stanisic (1996), *E. hewittorum* is herein reassigned to *Cineropa* on the basis of having similar protoconch sculpture to *Ci. roma* sp. nov. *Ci. hewittorum* differs from *Ci. roma* by the combination of smaller shell, more widely spaced radial ribs on the teleoconch and a smaller umbilicus. The additional records represent a range extension for the species.

Discocharopa Iredale, 1913

Discocharopa aperta (Möllendorff, 1888)

Common name. Miniscule White Pinwheel Snail.

New locality records in SCQ. Carnarvon NP: QMMO86613, Mount Moffatt peak; QMMO86590, Lot's Wife; QMMO86593, Racecourse Spring; QMMO86611, Saddler Spring; QMMO, 86592, Moolayember Gorge. Others. QMMO86615, Hilly Vale Stn, Arcadia Valley; QMMO86623, QMMO86620, QMMO86617, Palmgrove NP; QMMO86596, Fairview Stn; QMMO86627, Wallaroo Stn; QMMO86589, QMMO86584, QMMO86591, QMMO86628, MT Tabor Stn; QMMO86594, QMMO86595, Belbri Stn, Grafton Range.

Remarks. *Discocharopa aperta* is a widespread species in most of northern Australia preferring to live in dry vine thickets and lithorefugia. The species is characterised by dense radial ribbing on the teleoconch without traces of spiral sculpture, serrated interstitial microradial threads and a very wide saucer-shaped umbilicus. This combination of characters distinguishes the species from other small white charopids such as *Brigaloropa costulatai* sp. nov. *D aperta* also has an extensive distribution beyond Australia (Solem 1983).

DISCUSSION

Charopids from the south central Queensland brigalow lands have historically been poorly represented in museum collections. Reasons for this are many and diverse. Charopids are fundamentally a wet forest family in Queensland whose distribution attenuates from the coast to parts further inland. Hence, because of their low numbers and their extremely localised distributions, often in small and moister scattered patches of vine thicket in the SCQ region, charopids have been extremely difficult to collect: either alive (very rarely) or as dead shells recovered by sorting leaf litter.

As a consequence of the more intensive collecting efforts of C. Eddie, this study has shown that the SCQ brigalow region does support a relatively diverse charopid fauna. Nine genera (excluding *Discocharopa*) are represented in the cohort of species comprising this study. Seven genera are made up of regionally endemic taxa (*Spiraliropa, Brigaloropa, Arcadiaropa, Eddiea, Platyumbiropa, Carnaropa, Cineropa*) while two have extralimital connections further east (*Rhophodon, Tristanoropa*). Species vary in distribution from widespread (*Spiraliropa carnarvon*) to locally common (*Rhophodon moffatt, Carnaropa racecourse*) to uncommon and extremely localised (e.g. *Eddiea* spp., *Platyumbiropa* spp., *Brigaloropa costulata, Arcadiaropa sunnyholt*). Additional locality is presented for *Discocharopa aperta* which has a wider continental as well as extralimital distribution (Solem 1983, Stanisic *et al*. 2010).

The protoconch configurations of the genera documented in this study fall into the following categories: one spiral, four superior spiral, two radial, one superior radial and one finely cancellate. The differing superior spiral protoconch configurations involve subtle interpretations of the microarchitecture of the spiral elements. All are considered to represent separate generic-level lineages. Thus, the widely and regularly spaced rounded spiral cords of *Eddiea* are considered to be structurally distinct from the crowded, broad and regularly spaced flattish spiral cords of *Platyumbiropa* and the regularly spaced, wide and flat spiral cords of *Carnaropa*. These three configurations all differ dramatically from the crowded and wrinkled, spiral cords of *Cineropa*.

While the former approach may appear to be 'splitting hairs', the hypothesised evolutionary variability is within the domain of an ancient Gondwanan group of snails. The long-term history of charopids on the continent combined with their tiny size, moisture sensitivity and extremely low vagility (likely inter-generational existence under one log or rock) suggests that charopids in the semi-arid

FIG. 14. Charopid habitats (all SCQ). A-D, Vine thicket on basalt scree. **A,** Crowman Stn; **B**, Saddler Springs Stn; **C**, Grafton Range; **D**, Mt Tabor Stn. **E**, Vine thicket on sandstone, Waddy Brae Stn; **F**, Woodland, Bungil Creek floodplain, north north-west of Roma. Images: C. Eddie.

brigalow have been subject to many episodes of climate induced habitat reduction and fragmentation. Continental xerification that began in the Miocene would have begun the gradual isolation of moist refugia in the semi-arid brigalow lands which would in turn have caused some widespread ancestral populations to fragment. Over millennia, and driven by local and varied environmental pressures, local radiations would have developed from these ancestral species'clusters. Continued continental drying in the Plio-Pleistocene would have caused further population fragmentation leading to present day distribution patterns.

It is also reasonable to assume that some extinctions would have occurred. The roughly circumscribed geographic patterns displayed by each of the four superior spiral genera offers broad support for the preceding scenario. The broad similarity in the shells of these four genera is considered to indicate descent from a common ancestor. In contrast, the widespread occurrence of *Spiraliropa carnarvon* in isolated vine thicket patches attests to the past connectivity of this vine thicket archipelago.

The fact that most of this charopid fauna, with the possible exception of *Cineropa* spp. and to a lesser extent *Carnaropa* spp., is confined to small and scattered vine thicket patches, suggests that the current inventory of 18 species will surely increase with additional targeted field work and litter sorting. That will probably also increase the generic diversity of the SCQ charopids and only at that stage will this fauna be able to be put into biogeographic context. On the downside, the extremely localised distribution of many brigalow charopids, brings into sharp focus the inescapable fact that the large-scale land clearing of the brigalow in the past, has led to the extinction of some species.

The charopids of eastern Australia remain relatively poorly known and comprise many more undescribed species in museum collections than have been formally documented. The recently published studies on the MEQ charopids is a case in point (Holcroft 2018b, 2018c; Holcroft & Stanisic 2018). Collectively those studies elevated the number of known charopids from that region from 12 to 37 species based solely on material housed in museum collections. Hence, it is not surprising that 15 new species are described from SCQ. More than 450 undescribed species of charopids from wet, humid east coast rainforests are languishing in eastern state museum collections (QM, AM, MV) awaiting study. These include more than 80 from the Wet Tropics Bioregion alone that are housed in the Queensland Museum (Stanisic pers. obs.).

ACKNOWLEDGEMENTS

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LITERATURE CITED

Burch, J. B. 1976. Outline the classification of Australian terrestrial molluscs (native and introduced). *Journal of the Malacological Society of Australia* **3:** 127-156 https://doi.org/10.1080/00852988.1976.10673889.

Kershaw, R. C. 1955. Studies on the Australian Charopidae. *Victorian Naturalist* **72**: 28-30.

Hedley, C. 1924. Some notes on Australian land shells. Australian Zoologist **3**: 215-222.

Holcroft, L. 2018a. Protoconch sculpture as a taxonomic tool in Australian charopid systematics (Gastropoda: Eupulmonata: Charopidae). *Molluscan Research* **38**: 258-273 https://doi.org/10.1080/13235818.2017.1409069.

Holcroft, L. 2018b. A revision of *Gyrocochlea*-grade Charopidae from mid-eastern Queensland and redescription and generic reassignment of three *Gyrocochlea*-grade species (Eupulmonata: Charopidae). *Memoirs of the Queensland*

Museum-Nature **61**: 1-28 https://doi.org/10.17082/j.2204-1478.61.2018.2017-14.

Holcroft, L. 2018c. A revision of Charopidae with a finely cancellate protoconch sculpture from mid-eastern Queensland. (Eupulmonata: Charopidae). *Memoirs of the Queensland Museum-Nature* **61**: 83-107 https://doi.org/10.17082/j.2204-1478.61.2018.2018-09.

Holcroft, L. & Stanisic, J. 2018. Thirteen new charopid land snails from mid-eastern Queensland rainforests (Gastropoda: Eupulmonata: Charopidae). *Memoirs of the Queensland Museum-Nature* **61**: 155-186 https://doi.org/10.17082/j.2204-1478.61.2018.2018-11.

Hyman, I.T. & Stanisic, J. 2005. New charopid landsnails, chiefly from limestone outcrops in eastern New South Wales (Eupulmonata: Charopidae). *Memoirs of the Queensland Museum* **50**: 219-302.

Iredale, T. 1937. A basic list of the land Mollusca of Australia. Australian Zoologist **8**: 287-333.

Iredale, T. 1941. Guide to the land shells of New South Wales. Part II *Australian Naturalist* **10**: 262-269.

Shea, M., Colgan, D. & Stanisic, J. 2012. Systematics of the land snail genus *Gyrocochlea* and its relatives. (Mollusca: Charopidae). *Zootaxa* **3585**: 1-109 https://doi.org/10.11646/zoootaxa.3585.1.1.

Smith, B. J. 1992. Non-marine Mollusca. Pp.1-405. In Houston, W.W.K. (ed.), '*Zoological Catalogue of Australia* '. (Australian Government Printing Service: Canberra).

Smith, B. J. & Kershaw R. C. 1979. *Field guide to the non-marine molluscs of south eastern Australia*. Australian National University Press: Canberra. 285 pp.

Solem, A. 1983. Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part II. Families Punctidae and Charopidae, *Zoogeography*. (Field Museum: Chicago) https://doi.org/10.5962/bhl.title.2553.

Stanisic, J. 1990. Systematics and biogeography of eastern Australian Charopidae (Mollusca, Pulmonata) from subtropical rainforests. *Memoirs of the Queensland Museum* **30**(1): 1-241.

Stanisic, J. 2016: Two new species of Pinwheel Snail from contrasting Queensland habitats and a redescription and generic re-assignment of *Gyrocochlea myora* Stanisic, 2010 (Gastropoda: Eupulmonata: Charopidae). *Memoirs of the Queensland Museum-Nature* **60**: 1-12 https://doi.org/10.17082/j.2204-1478.60.2016.2016-07.

Stanisic, J., Shea, M., Potter, D. & Griffiths, O. 2010. *Australian land snails. Volume 1. A field guide to eastern Australian species*. (Bioculture Press: Mauritius). xii+591pp.

Stanisic, J., Shea, M., Potter, D. & Griffiths, O. 2018. *Australian land snails. Volume 2. A field guide to southern, central and western species*. (Bioculture Press: Mauritius). xiv+594pp. [Published 2017 but not officially distributed until June 2018]

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Late Devonian antiarch remains (placoderm fish) from the Gilberton Formation, north Queensland

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ABSTRACT

New Devonian fish remains are described from the lower part of the Gilberton Formation of north Queensland, the first identifiable specimens found since the original specimen was described in 1936. They include the first determinable dermal skull bones from this deposit. Some dermal bones of the trunk armour are closely associated, and of similar size with morphology consistent with coming from the same fish, permitting a provisional reconstruction of the ventral wall of trunk armour. The new morphological evidence indicates a form close to the antiarch *Remigolepis*, and a likely age of late Famennian for the lower fossiliferous strata of the Gilberton Formation.

❑ *Devonian fish; placoderms; antiarchs; Remigolepis; Gilberton Formation; Famennian*

The Devonian-?Carboniferous Gilberton Formation was named by White (1959, 1965) for a fluviatile deposit composed of siltstones, sandstones and conglomerates in the Gilberton Basin of north Queensland (Fig. 1). It covers about 120 km^2 in three separate outcrops (Withnall *et al*. 1980). Some other similar sedimentary rocks that underlie Carboniferous volcanics to the north of the Gilberton type area have been provisionally assigned to the unit (Withnall & Hutton 2013).

The fossiliferous lower part of the formation comprises interbedded quartzose and feldspathic sandstone and siltstone, likely deposited in a proximal braided stream system (Withnall *et al*. 1980). Plant fossils are relatively common, dominated by the lepidodendroid *Leptophloeum australe*, as described by M. White in White (1965). Vertebrate fossils, however, are extremely rare. A single placoderm plate impression was described by Hills (1936) as the posterior median dorsal plate of an antiarch placoderm, and was the first Australian record of this group attributed to the Middle Devonian. This specimen came from the southern outcrop of the Gilberton Formation, south of the Gilbert River (Fig. 1). Withnall *et al.* (1980) reported a further collection of "several plates, scales, a fragment of a spine, and an otolith [sic]" from low in the Gilberton Formation. They did not specify localities, and cited Dr Alex Ritchie (pers. comm., 1976) that the specimens were unidentifiable. The whereabouts of these samples is unknown.

In this paper we describe the first identifiable fish remains from the Gilberton Formation to be found since the original specimen was collected in 1934, including the first bones from the head of the fish. All the fish specimens belong to antiarch placoderms, a major subgroup of the Placodermi (extinct 'armoured

fishes'), the most diverse group of fossil fishes from the Devonian Period (Young 2008, 2010a).

The precise age of fossiliferous strata in the Gilberton Formation has been uncertain, as the plant taxa reported show varying ranges. Hills (1936) assigned a Middle Devonian age, but Withnall *et al.* (1980) considered that the balance of evidence supported a Late Devonian (Famennian) age for the lowermost levels, with the higher unfossiliferous strata possibly extending into the Early Carboniferous. However, Wyatt and Jell (1980) considered it more likely that the Gilberton Formation was entirely Late Devonian, because earliest Carboniferous sandstones elsewhere in North Queensland had different lithology, perhaps reflecting climate change across the Devonian-Carboniferous boundary. Our new fossil fish evidence also supports a Late Devonian age (see below).

STRATIGRAPHIC SETTING

No type section was defined for the Gilberton Formation, but two representative sections were described by Withnall *et al.* (1980; also in Wyatt & Jell 1980). The first reference section, in the southeastern part of the main outcrop area north of the Gilbert River (Fig. 1), comprises over 200 m of arkosic sandstones, with flaggy green and purple ferruginous siltstones in the lowermost 8 m producing plant remains including *Leptophloeum australe* (White 1965). The 200 m thickness was considered a local minimum for this area (Withnall *et al.* 1980), but the absence of marker beds makes total thickness for the main outcrop area difficult to estimate. However, Wyatt and Jell (1980) considered it unlikely to be much greater than 200 m.

The smaller outcrop south of the Gilberton River (Fig. 1), which produced the fossil fish described below, is the only outcrop that is not fault-bounded. A second representative section of about 150 m thickness was described by Withnall *et al.* (1980; also Wyatt & Jell 1980). The locality producing the fossil fish is close to the base of this reference section. The base of the Gilberton Formation, exposed at the eastern end of Commissioners Hill, rests unconformably on Proterozoic metavolcanics. The section extends from here to the highest preserved part of the Gilberton Formation about 1 km to the east-southeast. In the southern outcrop area, as in the main area to the north, the lowermost siltstone-bearing part of the Gilberton Formation is no more than about 10 m thick (Withnall *et al.* 1980). Most of this reference section comprises interbedded mid-brown, olive-green and purple lithic sandstones and subordinate siltstones (Withnall *et al.* 1980).

MATERIALS AND METHODS

The specimen (UQF13909) described by Hills (1936) was collected by de V. Gipps during survey work in 1934. The new specimens described here were collected in the same vicinity ('Fossil Gully', CJB19/04) by CJB, Bruce Burrow, John Armstrong and Ian Hutchings in May 2019. The plates are preserved as weathered bones and impressions in sandstone blocks collected as float in the gully. The bone is dark when fresh, and light in colour after weathering. The rock matrix is very hard siliceous sandstone or quartzite. Casts of the bone impressions were made with Pinkysil®, whitened with ammonium chloride, then photographed with a SZ40 Olympus dissecting microscope and DP12 imaging system. However, the best images were obtained by direct photography of the original impressions. Specimens are reposited in the Queensland Museum collection (QM F).

Abbreviations. Institutional abbreviations are as follows: UQF, University of Queensland Geology Department fossil collection [now part of the QM F collection]; QM, Queensland Museum.

We have used standard abbreviations for the dermal bones ('plates') of antiarch placoderms in the text and figures as follows: AMD, anterior median dorsal plate; AVL, anterior ventrolateral plate; MV, median ventral plate; Nu, nuchal plate; PDL, posterior dorsolateral plate; PL, posterior lateral plate; PMD, posterior median dorsal plate; PVL, posterior ventrolateral plate; SM, submarginal plate. Other abbreviations used in the figures are given in figure captions.

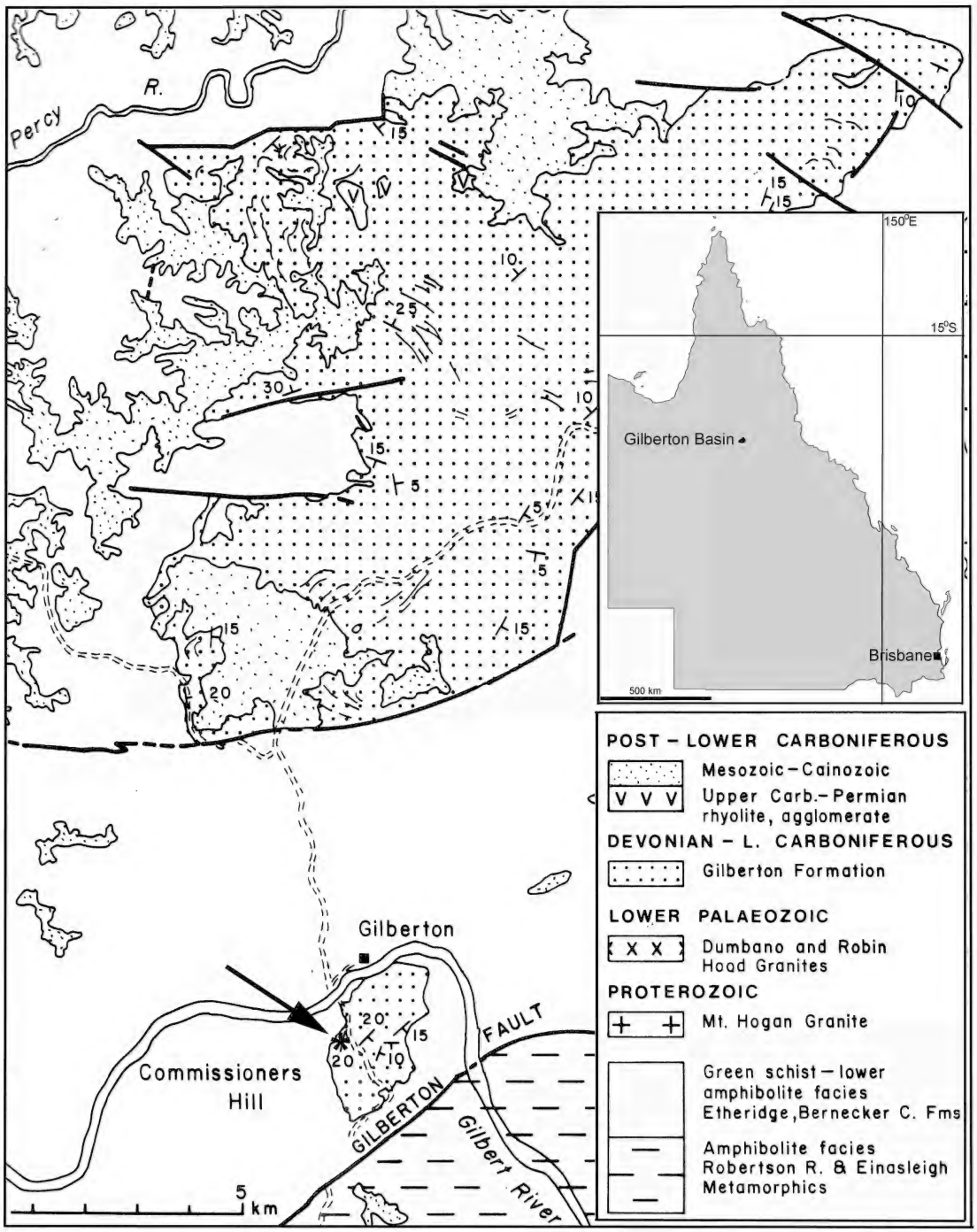

FIG. 1. Locality map of the Gilberton Formation outcrop in the Gilberton Basin of north Queensland (inset). Geological map modified from Wyatt & Jell (1980, fig. 12). Locality for the fossil fish remains in the Commissioners Hill area south of the Gilbert River indicated by an asterisk and arrow.

Proportions of antiarch dermal bones are normally expressed as breadth divided by length or vice-versa multiplied by 100 to give a 'breadth/length' or 'length/breadth' index. This is abbreviated to B/L or L/B index.

SYSTEMATIC PALAEONTOLOGY

Subclass PLACODERMI M'Coy, 1848

Order ANTIARCHI Cope, 1885

Family REMIGOLEPIDAE Stensiö, 1931

cf. *Remigolepis* sp. indet.
(Figs. 2, 3, 4, 5A, 6A-B)

1936 Antiarch: Hills, p. 163, fig. 3.
1958 *Asterolepis:* Hills, p. 89.
1960 antiarchan fish remains: Hill and Denmead, p. 154.
1961 antiarchan: White, p. 14.
1962 *Antiarchan:* White, p. 7.
1965 Antiarchan: White, p. 62, table 5.
1967 antiarchan fish: Hill, p. 615.
1967 *Asterolepis?*: Hill et al., p. d30, pl. DXV, fig. I.
1968 *Asterolepis*: Gilbert-Tomlinson, p. 207.
1973 Antiarchan fish remains: Smart, p. 7.
1978 *Asterolepis* sp.: Denison, p. 113.
1980 Antiarchan (Placoderm): Withnall et al., p. 79
1981 *Bothriolepis?* sp.: Young & Gorter, p. 90.
1982 *Bothriolepis*? sp.: Turner, p. 600.
1983 "antiarch plate … may belong to … *Bothriolepis*": Young, p. 71.
1990 antiarch: Young, p. 35.
1991 "probably a *Bothriolepis* plate": Long, p. 363.
2000 "dorsal plate of a placoderm": Turner, Basden & Burrow, p. 487.
2013 "fish fragments": Withnall & Hutton, p. 103.

Material. One posterior median dorsal plate (UQF13909); one nuchal plate (QM F 60156a,b); one submarginal plate (QM F 60150); two anterior ventrolateral plates (QM F 60151, 60152a,b); two posterior ventrolateral plates QM F 60153, 60154); one indeterminate impression, possibly an incomplete posterior ventrolateral plate (QM F 60155).

Remarks. In the dermal skull roof of *Bothriolepis* and related antiarchs (family Bothriolepidae), the nuchal plate reaches to the orbito-nasal fenestra on either side of a small post-pineal bone. However, the new nuchal plate from the Gilberton Formation lacks orbital facets, demonstrating that it was separated from the orbito-nasal fenestra by a large post-pineal bone (unknown). This is a primitive character seen in asterolepid antiarchs and various other antiarch sub-groups. Of four described antiarchs from the Upper Devonian of Australia, *Grenfellaspis* Ritchie *et al.* (1992) has a different skull shape and ornament with an elongate nuchal (family Sinolepidae). Three other non-bothriolepid antiarchs, two grouped in the family Pambulaspidae, have been named from the Australian Upper Devonian. *Pambulaspis* Young (1983) differs in the broad obtected nuchal area across the skull margin and the configuration of the sensory grooves. *Merimbulaspis* Young (2010b) has a distinctive ornament of anastomosing tuberculate ridges, which is completely different to the ornament in this new material. Two species of the genus *Remigolepis* Stensiö 1931 (family Remigolepidae) have been described from Australia: *R. redcliffensis* Johanson (1997a) and *R. walkeri* Johanson (1997b). Only in *Remigolepis* do we see similar characters for the nuchal plate as described below. In addition, the associated anterior ventrolateral plate from the trunk armour has a large anterior embayment indicating paired rectilinear semilunar plates, as also occur in *Remigolepis*. In *Asterolepis* this bone is paired, but quite different in shape. In bothriolepids the semilunar plate is unpaired.

We have assigned the small number of antiarch placoderm bones described below to cf. *Remigolepis* sp. indet., because there are numerous undescribed 'remigolepid'-like bones documented from many localities in the Upper Devonian of Australia (e.g. Young *et al.* 2010), with a distinct likelihood that new genera will be described in the future.

Age. Late Devonian (Famennian), Gilberton Formation.

Description. Dermal bones of the head.

Nuchal (Nu). An almost complete Nu plate, QM F 60156a,b (Fig. 2), is the first antiarch skull bone recorded from the Gilberton Formation. It is preserved in part and counterpart split within the dark bone, the part of the specimen with most of the bone still intact (Fig. 2A), and the counterpart (Fig. 2B) effectively an external impression with a film of black bone. On the

left side, the middle pit line sensory groove (mp) runs from a notch on the lateral margin, and the endolymphatic duct openings are visible centrally (d.end), these structures best shown on the counterpart. Plate margins are complete except for the right side, where the posterolateral corner was sliced off by the rock saw. This shows an oblique section through the right side (Fig. 2C), revealing the transverse nuchal crest that delineated the inside of the posterior skull margin in antiarchs. This seems unusually deep (~4.5 mm), but the crest is normally deepest at the lateral edges of the Nu, where this bone sutures with the paranuchal plate, and is less prominent mesially (e.g. Stensiö 1931, fig. 15; Downs *et al*. 2019, fig. 3C).

The part of the specimen shows that the plate is strongly arched anteroposteriorly. The bone exposed on the surface cut by the rock saw is well preserved, showing the cancellous inner and compact outer layers (Fig. 2C). The cut has not sliced through any tubercles, but low widely spaced coarse tubercles, c. 1 mm diameter, are visible on the external impression. The cut section shows the middle pit sensory groove is

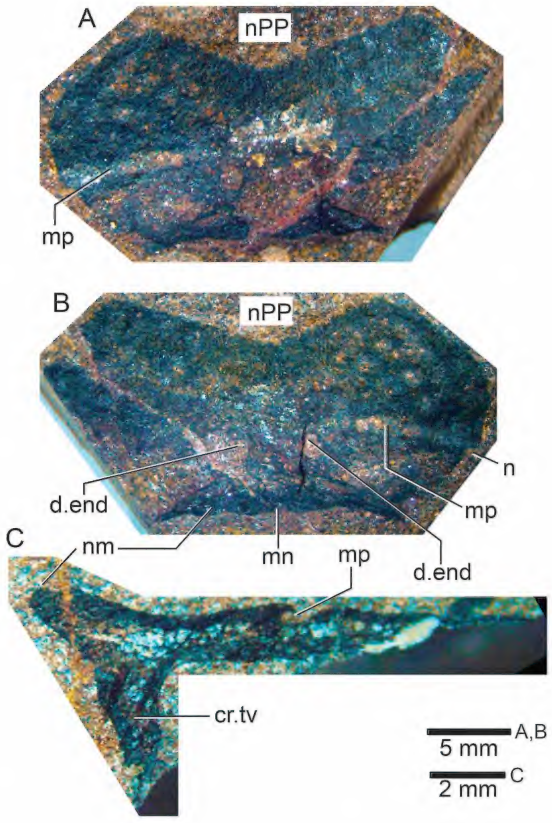

FIG. 2. cf. *Remigolepis* sp. indet., nuchal plate from the dermal skull roof (QM F 60156 a,b). **A**, dorsal view of the part; **B**, counterpart (rock impression with thin cover of bone); **C**, sawn section through the right posterolateral corner. Abbreviations: **cr.tv**, transverse nuchal crest; **d.end**, paired openings for endolymphatic ducts; **mn**, median notch; **mp**, middle pitline groove; **n**, notch; **nm**, obtected nuchal area; **nPP**, post-pineal notch.

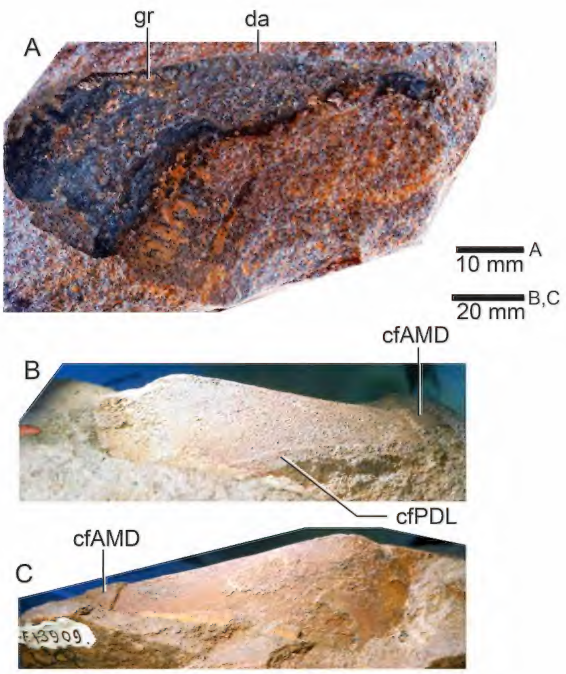

FIG. 3. cf. *Remigolepis* sp. indet. **A**, left submarginal plate from the head (QM F 60150); **B-C**, UQF13909, a posterior median dorsal plate from the trunk armour first described by Hills (1936) in right (**B**) and left (**C**) lateral views. Abbreviations: **cfAMD**, contact face for overlap of the anterior median dorsal plate; **cfPDL**, contact face for overlap of the posterior dorsolateral plate; **da**, dorsal angle; **gr**, groove.

undercut posteriorly, as is normal in *Asterolepis* and *Remigolepis* (but not in *Pambulaspis*; Young 1983). The obtected nuchal area (nm) is slightly inflected upwards to the posterior margin of the bone. The posterior face of the Nu is slightly concave, and about 6 mm deep to the ventral edge of the transverse nuchal crest. Externally the obtected nuchal area forms a narrow depressed strip along the posterior margin (nm, Fig. 2B). There seems to be a posterior indentation or notch at the midline, rather than a posterior process as in some other forms. All angles of the perimeter of the margin are slightly rounded. The endolymphatic duct openings are c. 4 mm apart. Maximum length is ~13 mm and maximum width estimated at 27 mm, giving a breadth/length (B/L) index of ~208. Midline length is c. 9 mm, and the posterior margin is c. 18 mm across.

As restored (Fig. 6A) the plate is short and broad with a shallow post-pineal notch. The B/L is within the range for most other antiarch species, as summarised by Young (1987, table 2). The broadest Nu listed was for *Asterolepis scabra* (B/L index 210), and in *Asterolepis alticristata* (Downs *et al.* 2019) it varies below and above twice as wide as long, but never exceeds a B/L of 210. Comparing various *Remigolepis* species, *R. kochi* is the broadest of the three named Greenland species (Stensiö 1931), but these are known by very few examples, so intraspecific variation is unclear. Similarly, the Australian species *R. redcliffensis* (Famennian from near Grenfell, NSW) is known by a single Nu plate (Johanson 1997a, fig. 9F-G). This is even broader (B/L index ~219), with a shallower postpineal notch than described here. However, this material is tectonically distorted so the bone could have been stretched laterally. Apart from slightly broader proportions, this specimen resembles QM F 60156 in that the middle pitline does not extend to the midline. Finer posterior pitlines are associated with the endolymphatic openings, but given the nature of preservation for QM F 60156 these would not be seen. The pitline configuration around the endolymphatic openings is again quite variable in other species (e.g. for *Asterolepis* see Stensiö 1931, fig. 13; 1948, fig. 64; Downs *et al.* 2019, figs. 3, 7).

Remigolepis walkeri Johanson (1997b) from the Frasnian at Canowindra NSW, is represented by many more specimens. As for *R. redcliffensis*, the middle pitline does not reach the midline, in contrast to some other species (*R. kochi* and *R. cristata* from Greenland, *R. zhongweiensis* and *R. microcephala* from China; Stensiö 1931, Pan *et al.* 1987). Nu proportions for *R. walkeri* are variable (B/L index 168, 188, 191 for three figured examples with the Nu well exposed). Another example is much more elongate (B/L index ~125; Johanson 1997b, fig. 6c), but again tectonic distortion (see Ritchie 2006) may have affected this. An isolated Nu plate from the Upper Devonian Hervey Group of NSW (Hills 1932, pl. 57, fig. 6) was first referred by Hills to 'Antiarchi indet.', but is clearly a *Remigolepis* as indicated by the associated trunk armour bones he described. This Nu plate also resembles QM F 60156 in being relatively broad (but the lateral corners are probably incomplete). It differs in that the post-pineal notch is deeper, and the middle pitlines extend close to the midline, where they are inflected posteriorly. However, the posterior margin seems relatively narrow, in that feature resembling the Gilberton nuchal.

The posterior margin being markedly narrower than across the lateral corners, and the stepped lateral margin at the level of the middle pitline, are distinctive features of QM F 60156, possibly indicating a new species.

Submarginal (SM). The second bone from the head (QM F 60150; Fig. 3A) is evidently a left SM plate ('extralateral plate' of earlier authors). This bone formed the operculum in antiarchs (Young 1984; Young & Zhang 1992), and other placoderms (Young 2010a). It is preserved mainly as an external impression, with faint ornament visible anterodorsally and a sheet of thin bone elsewhere. It has an ovoid shape, and is c. 41 mm long and 21 mm maximum height at about halfway along its length, where there is a slight angle (da) on the straightest edge. We interpret the straightest edge as dorsal, and the curved opposite margin as ventral, by comparison with other forms (e.g. *Remigolepis*;

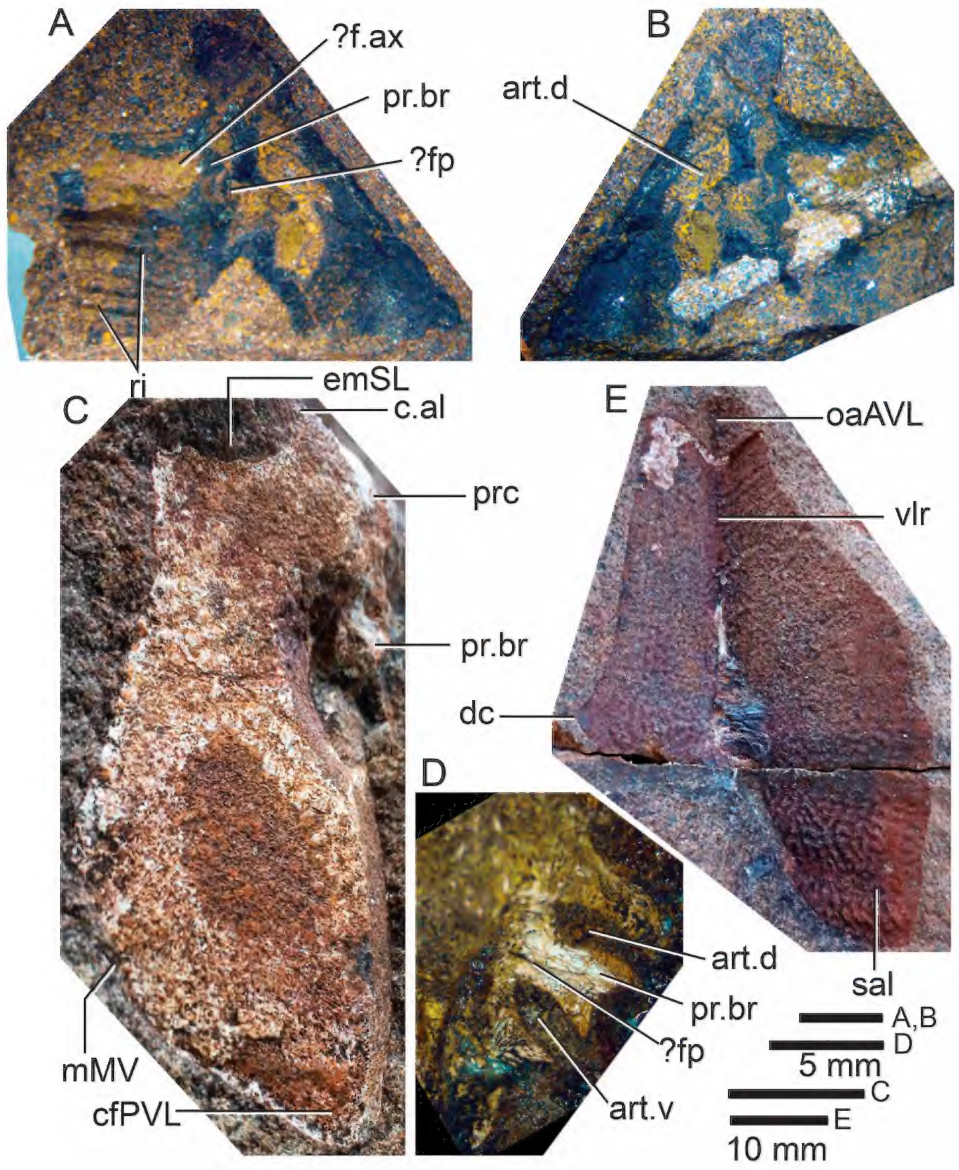

FIG. 4. cf. *Remigolepis* sp. indet. **A-B**, incomplete anterior part of an anterior ventrolateral plate in part and counterpart (QM F 60151). **C**, ventral view of a nearly complete left anterior ventrolateral plate (QM F 60152). **D**, enlarged ventrolateral view of the articular area for the pectoral appendage in QM F 60152. **E**, external impression of a left posterior ventrolateral plate (QM F 60153). Abbreviations: **art.d, art.v**, dorsal and ventral articular depressions to receive the proximal end of the pectoral appendage; **c.al**, anterolateral corner of AVL plate; **cfPVL**, contact face for overlap of the posterior ventrolateral plate; **dc**, dorsal corner of PVL lateral lamina; **emSL**, embayment that contained the semilunar plate; **f.ax**, axillary foramen of pectoral fin articulation; **fp**, funnel pit of brachial process; **mMV**, margin in contact with median ventral plate; **oaAVL**, overlap area for anterior ventrolateral plate; **pr.br**, brachial process for pectoral fin articulation; **prc**, prepectoral corner of AVL plate; **ri**, ridges; **sal**, subanal lamina of PVL plate; **vlr**, ventrolateral ridge of trunk armour.

Stensiö 1948, fig. 16). The slight angle presumably represents the articulation with the skull, as in the SM plates of *Asterolepis* (e.g. Karatajūtė-Talimaa 1963, fig. 32) and *Remigolepis* (Stensiö 1948, fig. 16). There is no evidence for a deep dorsal (spiracular) notch that occurs just in front of the articulation in *Pterichthyodes* and *Sherbonaspis* (Hemmings 1978; Young & Gorter 1981). Some *Asterolepis* spp. have the notch between a double articulation, and the notch may be much smaller or obscure in other forms (e.g. *Remigolepis*; Stensiö 1948, fig. 16; *Merimbulaspis*; Young, 2010b, fig. 4C, D).

The Gilberton SM is dorsoventrally convex. A thin low ridge delineating a shallow groove runs inside and parallel to the dorsal margin. An external ridge is developed behind the shallow dorsal notch in *Merimbulaspis*, and *Remigolepis walkeri* shows a stronger external ridge (e.g. Johanson, 1997b, fig. 3F). Internal ridges and grooves occur inside the dorsal margin of the SM in both *Asterolepis* and *Remigolepis*.

The anteroventral margin is not quite complete, but QM F 60150 is estimated at about twice as long as high. In other taxa, proportions of the SM vary; *Remigolepis walkeri* (Johanson, 1997b) has similar proportions to our new specimen. In the Greenland *Remigolepis* figured by Stensiö (1948, fig. 16) the SM has a more pointed anterior end, and a L/B index of about 210.

Dermal bones of the trunk armour.

Posterior median dorsal (PMD). The original specimen (UQF13909) is a PMD plate, preserved mainly as an internal impression. It was described by Hills (1936, p. 163) as follows: "The plate is 8 cm. long and approximately 5.6 cm. wide at the widest part, where it is probably incomplete. Anteriorly and laterally, the areas of overlap on to the anterior median dorsal and posterior dorso-laterals are clearly shown, the posterior edge being free."

Hills noted the absence of diagnostic characters (still the case), but accepting the geological age provided to him by F.W. Waterhouse, called this the first record of an antiarch from the Middle Devonian of Australia. Later, Hills (1958, p. 89) ascribed the generic name *Asterolepis* to the specimen, presumably by comparison with European sequences, and this entered the international literature (e.g. Denison 1978, p. 113). Hills noted however that the Gilberton example was younger than the marine Middle Devonian fishes of eastern Australia (now known to be Early Devonian), and could even be Upper Devonian (*Asterolepis* in Europe has a stratigraphic range of Middle-Upper Devonian).

As restored by Hills (1936, fig. 3) this plate is relatively elongate, with a B/L index of 82, comparable to the PMD plates in restorations of *Remigolepis* (82 for Greenland; Stensiö 1931 fig. 80; 88 for *R. walkeri*; Johanson 1997b, fig. 20a). Similar variation (76-100) occurs in *Asterolepis* (e.g. Karatajūtė-Talimaa 1963, p. 163). There is little to add to Hills' description, the PMD plate being generally similar in different antiarch taxa. For the first time here we illustrate lateral views of the specimen, to show the convex inner surface (Fig. 3B-C).

The new examples of trunk armour bones described below all come from the ventral wall of the trunk armour, and represent at least two individual fish. There are two anterior and two posterior ventrolateral plates, all from the left side.

Anterior ventrolateral (AVL). QM F 60151a,b, is a very incomplete anterior portion of the lateral lamina of an AVL from the left side. It is preserved in part and counterpart broken through the articular region for the pectoral fin (Fig. 4A-B). The bone has a steeply inclined anterior margin, presumably the anterior edge of the lateral lamina of the AVL. If not fractured, then this appears more steeply inclined than in *Bothriolepis macphersoni* (Young 1988, fig. 56), or *Remigolepis* AVLs from Greenland (e.g. Stensiö 1931, pl. 24, figs 2,4). Part of the ventral surface and the brachial process are visible; the distal end of the latter is possibly preserved inside the rock. A rounded space may represent the funnel pit (fp) inside the brachial process. According to Johanson (1997a) the funnel pit is much larger in *Remigolepis redcliffensis* than in the Greenland *Remigolepis*, but the latter are preserved as eroded AVLs, so this difference is not clearly demonstrated.

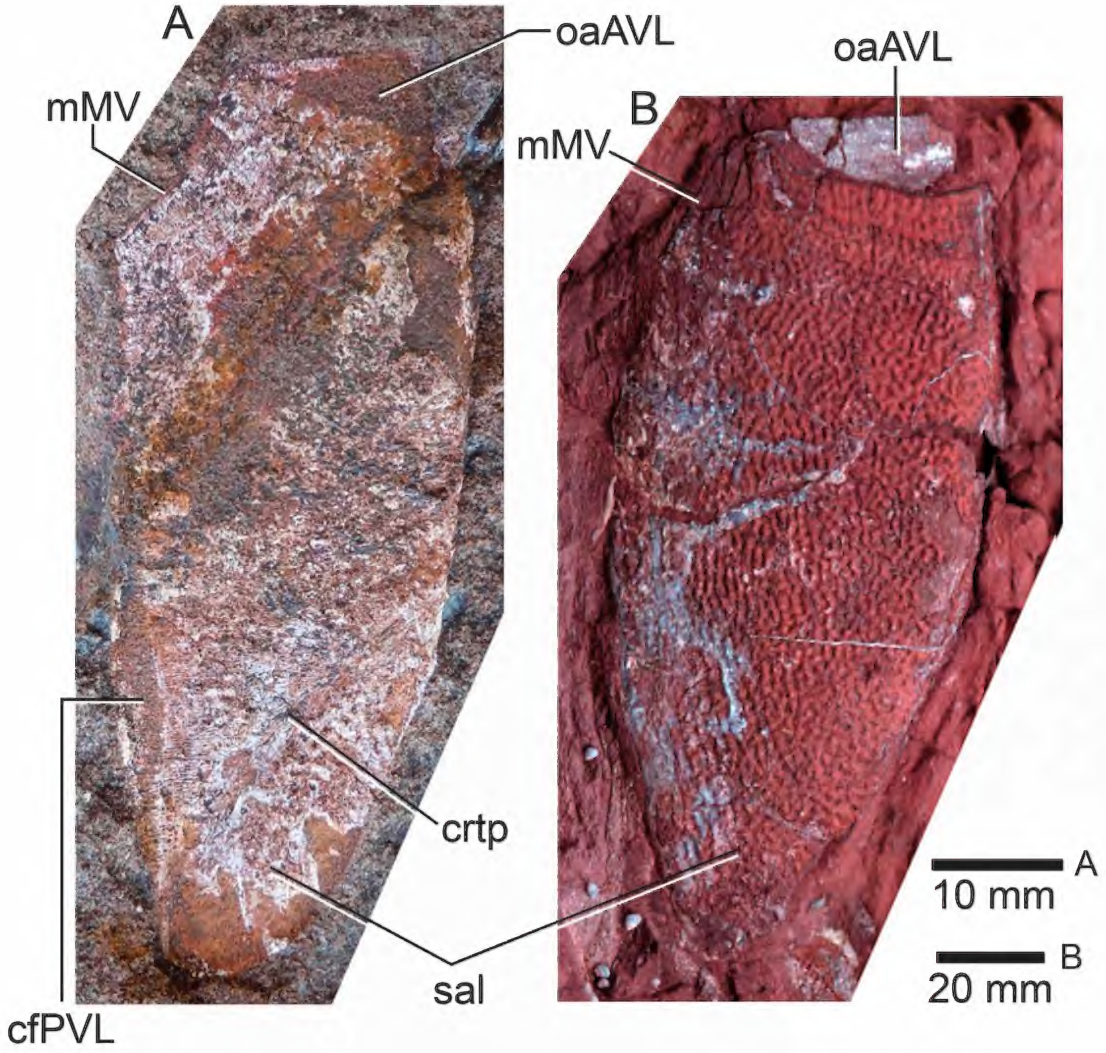

FIG. 5. Remigolepid left posterior ventrolateral plates in ventral view. **A**, cf. *Remigolepis* sp. indet. (QM F 60154) from the Gilberton Formation, showing the impression of the internal surface in ventral view. **B**, *Remigolepis* sp. nov. from the Worange Point Formation at Boyds Tower south of Eden, NSW far south coast (uncollected specimen in outcrop, showing the ornamented external surface in ventral view). Abbreviations: **cfPVL**, contact face for overlap with opposite posterior ventrolateral plate; **crtp**, posterior internal transverse crest of trunk armour; **mMV**, margin in contact with median ventral plate; **oaAVL**, overlap area for anterior ventrolateral plate; **sal**, subanal lamina of PVL plate.

In QM F 60151 the brachial process (pr.br) shows striations indicating the inner bone tissue is exposed. The axillary foramen is of distinctive size and shape for different genera, but it is unclear on this specimen. An area of rock matrix surrounded by bone (?f.ax) is an opening in about the correct position (cf. Young 2008, fig. 2A), so it may include this structure. Beneath is a series of distinct longitudinal ridges, which can be compared with strong ridging of the ornament in the same position on an AVL plate of *Remigolepis redcliffensis* illustrated by Johanson (1997a, fig. 11G). The axillary foramen in that species is very small.

QM F 60152 (Fig. 4C) is the most complete AVL. It is partly an internal impression, maximum length 55 mm, with most covered by a poorly preserved sheet of bone. Most of the ventral lamina is preserved, except for the anterolateral corner of the subcephalic division, which has broken off at the edge of the block. Thus, the prepectoral (prc) and anterolateral (c.al) corners of the AVL are incomplete. The lateral lamina, mainly an impression, includes a broken brachial process for the pectoral fin articulation (pr.br). The posterior overlap with the PVL is preserved as a very faint contact face on the inner surface, visible because most of the bone has weathered away (cfPVL). The plate margin that contacted the MV is 13 mm long, although the anterior corner is unclear. The margin that was overlapped with the opposite AVL is much longer (c. 30 mm) than the MV margin. In contrast, in *Sherbonaspis hillsi* this margin is relatively shorter (Young & Gorter 1981, fig. 18). The margin for the semilunar plate forms a deep embayment (emSL; not quite complete because the anterolateral corner is missing).

Unusual for an AVL is that the ventral lamina is broadest (22 mm) at the level of the anterior point of the MV, and narrows anteriorly, being only c. 10 mm wide at the level of the pectoral fin joint. Stensiö (1948, p. 134) distinguished the AVL of *Bothriolepis* from *Pterichthyodes*, *Asterolepis* and *Remigolepis* by the ventral lamina being broadest at the level of the prepectoral corner (prc), whereas in the other three genera it is broadest more posteriorly, as in QM F 60152. Even so, for *Pterichthyodes* (Hemmings 1978, pl. 2), and *Sherbonaspis* (Young & Gorter 1981, fig. 18A,C) the ventral lamina of the AVL tends to be of similar width for the whole length. This is also the case for *Remigolepis* from the type locality in East Greenland, and also Canowindra, New South Wales (Stensiö 1931; Johanson 1997b, figs. 19, 20c). The holotype specimen of *R. redcliffensis* (Johanson 1997a, fig. 11A) is broadest at a similar level to QM F 60152, but that material is tectonically distorted, and other proportions of that bone are quite different to the specimen described here. However AVL plates with similar shape are seen in various species of *Asterolepis*, where the lateral edge of the trunk armour is more obtuse and the AVL is more obliquely oriented. Examples are *Asterolepis scabra* (Nilsson 1941, fig. 7) and *A. ornata* (Gross 1931, fig. 19; Karatajūtė-Talimaa 1963, fig. 36). Even in some *Remigolepis* species with an obtuse armour, the AVL has been restored as largely parallel-sided (e.g. *R. zhongningensis*; Pan *et al*. 1987, fig. 30).

Generally in antiarchs the right AVL overlaps the left, so there should be an overlap area on the external surface, but there is no indication of this on this specimen. The overlapped part is much thinner than the main bone, so possibly this has broken off, partly explaining the narrow ventral lamina at this level.

The AVL plate in antiarchs projects forward under the head (the 'subcephalic division' of *E. Stensiö*), forming the floor of the branchial chamber. Towards the front of the AVL, the inner surface always has a distinct ridge or crest (the 'postbranchial lamina') that delineated the posterior wall of the branchial chamber. The numerous examples of *Remigolepis walkeri* from Canowindra NSW (at least 1780 articulated specimens; Ritchie 2006) are mainly preserved as external impressions, so this internal structure is visible in only a few examples (mislabelled as the internal anterior transverse crista by Johanson 1997b, fig. 13a). Better preserved *Remigolepis* (e.g. the holotype of *R. armata*; Lukševics 1991, pl. 1, fig. 8a) show the postbranchial lamina as a strong vertical crest crossing diagonally to the internal corner on the AVL plate within the semilunar notch (also Moloshnikov 2008, pl. 3, fig. 14). Similar

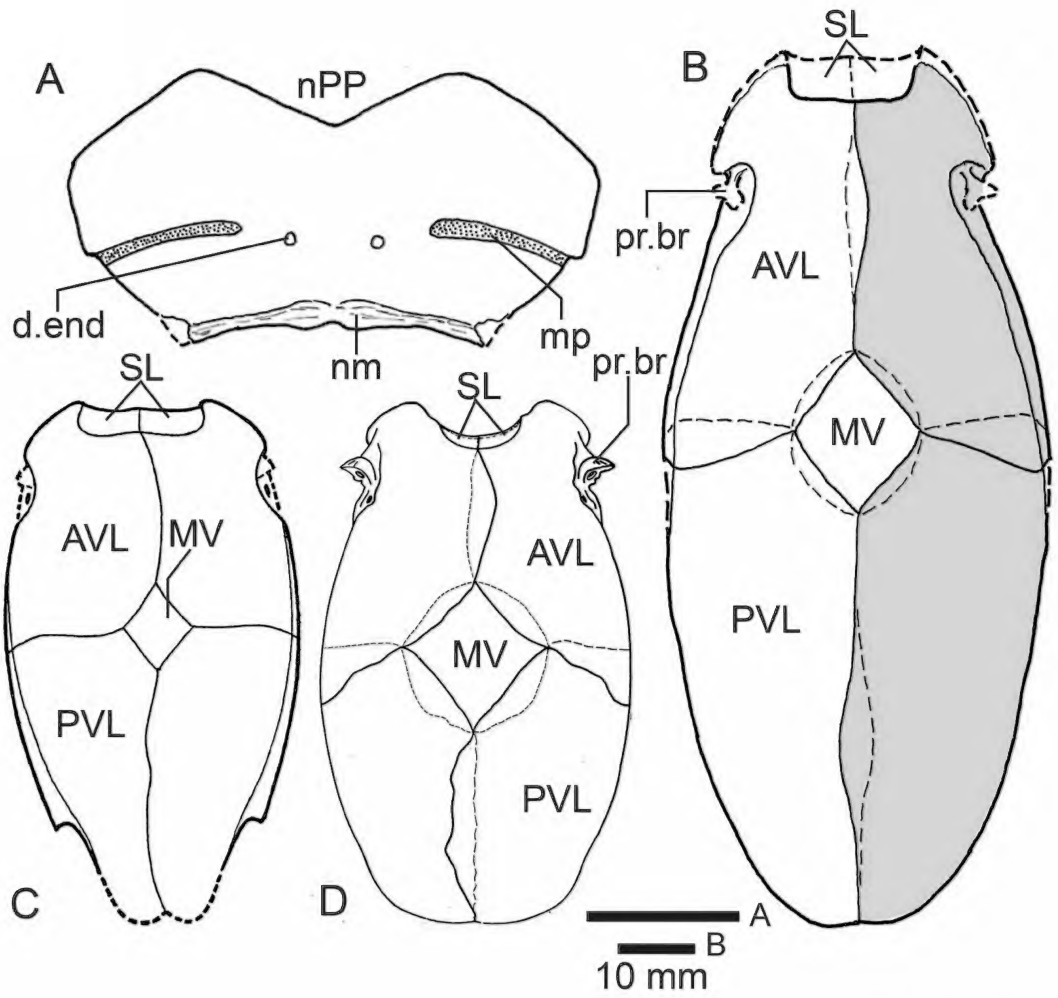

FIG. 6. **A**, cf. *Remigolepis* sp. indet., reconstruction of the nuchal plate from the dermal skull roof (based on QM F 60156 shown in Fig. 2); **B**, cf. *Remigolepis* sp. indet., provisional restoration of the ventral wall of the trunk armour (preserved areas shaded), based on QM F 60152 (Fig. 4C), and QM F 60154 (Fig. 5A). **C**, *Remigolepis* sp., ventral trunk armour restoration (modified from Denison 1978, after Stensiö 1969); **D**, *Asterolepis ornata*, ventral trunk armour restoration (modified from Karatajūtė-Talimaa 1963, fig. 36) (C, D not to scale). Abbreviations: **AVL**, anterior ventrolateral plate; **d.end**, paired openings for endolymphatic ducts; **mp**, middle pitline groove; **MV**, median ventral plate; **nm**, obtected nuchal area; **nPP**, post-pineal notch; **pr.br**, brachial process of pectoral fin articulation; **PVL**, posterior ventrolateral plate; **SL**, semilunar plate.

preservation is seen in undescribed *Remigolepis* from the Famennian of the NSW south coast near Eden. However, there is no sign of this structure in QM F 60152 as preserved. This region is covered with weathered bone, so the inner surface is not exposed, and we assume therefore that the postbranchial lamina is preserved inside the rock.

QM F 60152 retains a partly eroded brachial process which carried the pectoral fin articulation (pr.br, Fig. 4C). A more lateral view (Fig. 4D) shows better detail of the articular area. The eroded brachial process shows a central line, possibly a crack, but more likely the very edge of the funnel pit (fp), and a conical cavity within the brachial process interpreted to

have contained the cartilaginous remnant of the scapulocoracoid that articulated with the internal pectoral fin skeleton (Young & Zhang 1992; Young 2008). Deep articular depressions around the brachial process received the rounded proximal end of the dermal pectoral appendage, and as exposed in this section (art.d, art.v) may be compared with similar preservation in an eroded AVL plate from Greenland (Stensiö 1931, pl. 24, fig. 2).

Posterior ventrolateral (PVL). On the same bedding plane and block as QM F 60152 are two PVL plates of different shapes. QM F 60153, which is 160 mm distant from the AVL, is preserved as an external impression, and is also from the left side (Fig. 4E). The lateral lamina is quite complete, highest posteriorly (c. 16 mm) at its dorsal corner (dc), and reducing to c. 7 mm high at the level of the overlap area for the AVL (oa.AVL). The lateral lamina length (excluding the overlap area) is c. 36 mm, but the posterior margin is obscured by a crack through the rock. The ventral lamina is at least 52 mm long (excluding the anterior overlap), with the subanal component c. 20 mm long. Its maximum breadth (c. 20 mm) is at the level of the posterior margin of the lateral lamina. The preserved mesial edge seems complete because the ornament alignment of tubercle rows parallels the edge. More anteriorly the edge is broken off, so there is no evidence of the length of the margin with the MV.

This plate closely resembles PVLs of *Bothriolepis* (e.g. Stensio 1948, figs 170-74; Young 1987, fig. 2C; Young 1988, figs 31A, 43G, 60), but given the associated remains it is assumed to belong to cf. *Remigolepis*. In *Remigolepis* the lateral lamina has a similar configuration to *Bothriolepis*, even though dorsally it is in contact with a different element, the PL plate. *R. kullingi*? from Greenland has similar lateral lamina proportions: ~15 mm high at the dorsal corner, reducing to 7 mm anteriorly (Stensiö 1931, pl. 13, fig. 4). Several other examples from Greenland are similarly developed (Stensiö 1931, fig. 90A; pl. 21, fig. 1; pl. 22, fig. 4). Stensiö (1931, pp. 177-78) noted that in the Greenland *Remigolepis* the PL plate partly overlaps the dorsal edge of the PVL, but that was not the case in QM F 60153, as the ornament goes right to the edge of the impression.

The second PVL impression (QM F 60154) is also from the left side, so represents a different fish to QM F 60153. However, it could have come from the same individual as the most complete AVL just described, being only 75 mm away on the same block. Both examples are similarly preserved with a thin white film of remnants of bone. QM F 60154 has some impressions of ornament but mainly shows the impression of the inner surface of the ventral lamina (Fig. 5A). The lateral lamina is not visible, if preserved being completely buried in the exceptionally hard matrix. Figure 5B compares a similarly preserved PVL of an undescribed *Remigolepis* species from the Famennian Worange Point Formation near Eden on the New South Wales south coast.

In the Gilberton PVL the ventral lamina appears almost complete, with total length of c. 72 mm. An overlap for the AVL is faintly visible (oaAVL). Its ornamented edge is of similar length to the corresponding edge of the nearby AVL (Fig. 4C), i.e. c. 13 mm, consistent with the two bones coming from the same fish. The length of the MV margin (c. 25 mm) is relatively short. In *Remigolepis redcliffensis*, Johanson (1997a) suggested that the MV was somewhat larger than in other *Remigolepis* species. At the level of the posterior corner of the MV, the ventral lamina of the PVL is c. 28 mm wide, and behind this breadth decreases gradually to the posterior margin of the subanal lamina (sal). The posterior half of the mesial margin shows faint overlap, about 5 mm wide, with the opposite PVL along a length of c. 20 mm. Generally in antiarchs the left PVL overlaps the right, so this would be an internal contact face (cfPVL). Maximum width of the contact face is at the level of the anterior end of the subanal lamina. A faint lineation within the texture of the weathered bone is suggestive of the posterior internal crista (crtp), which has a very oblique orientation. This internal crista crosses the subanal part of the ventral lamina, exactly as in *Bothriolepis* (e.g. Stensiö 1948, fig. 172C). The subanal lamina measures about 40 mm along its lateral edge.

On the assumption that this PVL is from the same individual as QM F 60152, a tentative reconstruction of the ventral wall of the trunk shield (Fig. 6B) can be compared with *Remigolepis* from the Famennian of Greenland (Fig. 6C) and *Asterolepis* from the Frasnian of Europe (Fig. 6D). For the Gilberton material, the proportional length of the AVL compared to the PVL (measured from the lateral corner of the MV plate) is about 78%. This is similar to some other restorations for *Remigolepis*, for example 78 from East Greenland (Stensiö 1931, fig. 87), and 77 for *R. walkeri* from Canowindra NSW (Johanson 1997b, fig. 20c). In other restorations the PVL is proportionately less elongate (90, 97 for two examples from East Greenland figured by Johanson 1997b, fig. 19), or 103 (the AVL slightly longer than the PVL) in *Remigolepis zhongningensis* from China (Pan *et al*. 1987, fig. 30). Similar variation is seen in the genus *Asterolepis*. For articulated examples from the Lode Quarry in Latvia, *Asterolepis ornata* varies between 81 and 87 (Lyarskaya 1981, pls. 21-23), and in *Asterolepis radiata* between 96 and 101 (Lyarskaya 1981, pls. 31-32).

In general, the restoration (Fig. 6B) based on the new Gilberton AVL and PVL plates has a larger MV, and is more narrow across the AVLs at the level of the pectoral fin articulation than in *Remigolepis* from East Greenland (Stensiö 1931, fig. 87), or *R. walkeri* from Canowindra (Johanson 1997b, fig. 20c). However more examples would be needed to clarify if these are valid species differences. Possibly, the relatively larger MV plate in *Remigolepis redcliffensis* (Johanson 1997a) distinguishes it from the Gilberton taxon, but *R. redcliffensis* resembles the new material in the similar Nu, and ridged area on the AVL plate. The deep rectangular anterior indentation indicates paired semilunar plates of similar shape (SL, Fig. 6B), as seems typical for various *Remigolepis* species. In contrast, these bones are smaller and of more 'semilunar' shape in various *Asterolepis* species (e.g. Gross 1931; Karatajūtė-Talimaa 1963; Lyarskaya 1981). Even though *Asterolepis* typically also has a large anterior embayment in the ventral trunk armour (Fig. 6D), of more rounded shape than in *Remigolepis*, the semilunar plates occupy only the posterior part.

The last specimen from Gilberton listed above (QM F 60156) is very incomplete, but is possibly another PVL. It shows an external impression including a 55 mm long external dorsolateral or ventrolateral ridge, with an overlap area which must be at the front of the plate. There is no sign of sensory grooves, so the plate cannot be a mixilateral or dorsolateral plate, and thus may be a PVL.

DISCUSSION

Antiarch classification and biostratigraphy

Asterolepis and *Bothriolepis*, two antiarchs with distinctive skull shapes from the 'Old Red Sandstone' facies of Europe, were erected by Eichwald (1840), and subsequently became the genotypes of two higher groupings – families Asterolepidae and Bothriolepidae (sometimes elevated to suborders). They also had different stratigraphic ranges: *Bothriolepis* was first described from the Famennian of Russia, and *Asterolepis* from the Frasnian of the Baltic (Eichwald 1840). *Asterolepis* was later discovered in many Middle Devonian localities (for a recent summary of the history of this genus see Newman *et al*. 2019). The replacement and stratigraphic overlap of *Asterolepis* by *Bothriolepis*, near or just above the Middle-Late Devonian boundary, became recognized as an important biostratigraphic horizon in the fish-bearing non-marine Devonian strata of western Europe (Young 1974). Stensiö (1931) described the new genus *Remigolepis* (placed in its own family) from the '*Remigolepis* Series' of East Greenland, a fossil assemblage made famous (Säve-Söderbergh, 1932; Jarvik, 1952, 1996) by the discovery of *Ichthyostega* and *Acanthostega*, the first Devonian tetrapods (land animals) from the fossil record. *Remigolepis* was unique, among antiarchs then known, in lacking a distal (elbow) joint in the pectoral appendage. Although *Remigolepis* closely resembles *Asterolepis* in the details of skull morphology (e.g. Stensiö 1931; Karatajūtė-Talimaa 1963; Lukševics 2001), the trunk armour differs in having separate

PDL and PL plates (fused into a single mixilateral plate in *Asterolepis* and *Bothriolepis*), and in the configuration of overlap areas on the AMD.

Various later authors (e.g. Denison 1978) rejected a separate family Remigolepidae on two arguments, morphological and stratigraphic: i) absence of the elbow joint was seen in aberrant *Asterolepis*, and ii) the age of the '*Remigolepis* Series' in East Greenland was late Famennian, so the absence of the distal pectoral fin joint was unlikely to have the significance accorded it by Stensiö (1931).

One year after that publication, Hills (1932), based on Stensiö's advice and relying on his unpublished manuscript, recorded the first *Remigolepis* from Australia (Hervey Range in central New South Wales). The Hervey Range material has never been properly collected and described, and there are numerous other undescribed occurrences of '*Remigolepis*' across Australia (e.g. Young 1993; Young *et al*. 2010). It was first assumed that *Remigolepis* in Australia indicated latest Devonian (Famennian), based on its northern hemisphere stratigraphic range, but this caused difficulties with local stratigraphy. Hills (1958) suggested that the placoderm genera *Bothriolepis*, *Phyllolepis* and *Remigolepis* did not have the temporal significance in Australia that they had in Europe. He suggested a 'dispersal centre in Asia', from which older *Bothriolepis* had been recorded. Later, the yunnanolepid antiarchs from China demonstrated an unjointed pectoral appendage in Late Silurian-Early Devonian assemblages, destroying argument (ii) mentioned above for placing *Remigolepis* within the family Asterolepidae. Nevertheless, Pan *et al*. (1987) documented new species of *Remigolepis* from the Upper Devonian of China (Ningxia Province), to which they assigned a Famennian age, again based on East Greenland occurrences. However, an associated spore assemblage may indicate an older age (even late Middle Devonian; see discussion in Ritchie *et al*. 1992, p. 364). For a recent summary comparing Chinese and Australian Devonian antiarch occurrences see Young and Lu (2020).

The most completely described *Remigolepis* preservation (from Australia, and the world), although only casts in sandstone, is *Remigolepis walkeri* Johanson (1997b) from Canowindra in central New South Wales. Canowindra was also first considered of Famennian age, but detailed mapping, and fossil fish and invertebrate collecting from many new sites, showed that it was older, of similar age to the late Frasnian marine transgression documented in Devonian sequences from both eastern and western Australia (Young 1999, 2006, 2007; Young *et al*. 2000). However, other *Remigolepis* occurrences, for example associated with the giant lobe-fin *Edenopteron* on the NSW south coast, are of late Famennian age as in East Greenland (e.g. Young 2007; Young *et al*. 2013, 2019). Subsequent *Remigolepis* discoveries in Europe and Russia (e.g. Lukševics 1991; Panteleyev 1992; Moloshnikov 2008) have all been in Upper Devonian (Famennian) strata.

Meanwhile, older asterolepid antiarchs (family Pterichthyodidae) in eastern Australia were documented from ?Early and Middle Devonian non-marine (Young & Gorter 1981) and marine limestone occurrences (Young 1990). Acid-prepared remains of an unnamed asterolepid antiarch from the Emsian Cravens Peak Beds limestone of the Georgina Basin in western Queensland (Young 1984b) evidently represent the world's oldest occurrence of the family Asterolepidae (see Young & Lu 2020).

Age of the Gilberton Formation fish

Described above is the first remigolepid antiarch documented from Queensland, and in the context of the preceding discussion this would be assigned a Late Devonian age, either Frasnian or Famennian. The lower fossiliferous beds of the Gilberton Formation also have abundant plant remains, mainly *Leptophloeum australe*, which in eastern Australia is most likely confined to the Late Devonian (see discussion in Dunstone & Young 2019), although other macroplants are of Carboniferous aspect (Withnall *et al*. 1980). Palynomorphs of the latest Famennian *Retispora lepidophyta* zone (Young 1996) are also recorded from some percussion drill-holes (Withnall *et al*. 1980). There is no evidence anywhere of antiarch placoderms younger than the Devonian-Carboniferous

boundary (e.g. Young 2010a), so the new fish evidence accords with the conclusion of Withnall *et al*. (1980, p. 79) that the lowermost part of the Gilberton Formation is of Late Devonian (Famennian) age. However, although *Remigolepis* in Europe is indicative of latest Devonian (Famennian), in Australia the genus occurs earlier, in the Frasnian at Canowindra, NSW (e.g. Young 1974, 1999), and probably at Genoa River in Victoria (Young 2007). Thus, on the fish evidence alone, a Frasnian age cannot be excluded for the Gilberton Formation.

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LITERATURE CITED

Denison, R.H. 1978. *Placodermi. Handbook of Paleoichthyology, volume 2*. Schultze, H.P. (ed.). (Gustav Fisher Verlag: Stuttgart).

Downs, J.P., Daeschler, E.B., Lo, N., Carey, E.N. & Shubin, N.H. 2019. *Asterolepis alticristata* n. sp. (Antiarchi) from the Upper Devonian (Frasnian) of Nunavut, Canada, and a report on the antiarch diversity of the Fram Formation. *Geodiversitas* **41**(1): 679–698. https://doi.org/10.5252/geodiversitas2019v41a19

Dunstone, R.L. & Young, G.C. 2019. New Devonian plant fossil occurrences on the New South Wales south coast: geological implications. *Australian Journal of Earth Sciences* **66**: 57-70. https://doi.org/10.1080/08120099.2018.1533495

Eichwald, E.I. von 1840. Die Thier- und Pflanzenreste des alten rothen Sandsteins und Bergkalks im Novgorodschen Gouvernment. *Bulletin of the Academy of Sciences, St Petersburg* **7**: 78-91.

Gilbert-Tomlinson, J. 1968. A new record of *Bothriolepis* in the Northern Territory of Australia. *BMR Bulletin* **80**: 189–224.

Gross, W. 1931. *Asterolepis ornata* Eichw. und das Antiarchi Problem. *Palaeontographica A* **75**: 162.

Hemmings, S.K. 1978. A monograph of the Old Red Sandstone antiarchs of Scotland: *Pterichthyodes* and *Microbrachius*. *Palaeontographical Society Monographs* **131**: 1–64.

Hill, D. 1967. Devonian of Eastern Australia. Pp. 613–630. *In* D.H. Oswald (ed.) *International Symposium on the Devonian System II*. (Alberta Society of Petroleum Geologists: Calgary).

Hill, D. & Denmead, A.K. 1960. The Geology of Queensland. *Journal of the Geological Society of Australia* **7**: 1–474.

Hill, D., Playford, G. & Woods, J.T. 1967. Devonian Fossils of Queensland. (Queensland Palaeontographical Society: Brisbane).

Hills, E.S. 1932. Upper Devonian fishes from New South Wales. *Quarterly Journal of the Geological Society of London* **88**: 850–858. https://doi.org/10.1144/GSL.JGS.1932.088.01-04.26

Hills, E.S. 1936. Records and descriptions of some Australian Devonian Fishes. *Proceedings of the Royal Society of Victoria* **48** (N.S.) 2: 161–71.

Hills, E.S. 1958. A brief review of Australian fossil vertebrates. Pp. 86-107. *In* T.S. Westoll (ed.) *Studies on Fossil Vertebrates*. (Athlone Press: London).

Jarvik, E. 1952. On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Meddelelser om Grønland* **114**: 1-90.

Jarvik, E. 1996. The Devonian tetrapod *Ichthyostega*. *Fossils and Strata* **40**: 1-213. https://doi.org/10.1111/j.1502-3931.1996.tb01839.x

Johanson, Z. 1997a. New antiarchs (Placodermi) from the Hunter Siltstone (Famennian) near Grenfell, N.S.W. *Alcheringa* **21**(3): 191–217. https://doi.org/10.1080/03115519708619173

Johanson, Z. 1997b. New *Remigolepis* (Placodermi; Antiarchi) from Canowindra, New South Wales, Australia. *Geological Magazine* **134**: 813-846. https://doi.org/10.1017/S0016756897007838

Karatajūtė-Talimaa, V. 1963. Rod *Asterolepis* iz devonskikh otlozheniy Russkoy platformy. [The genus *Asterolepis* from the Devonian deposits of the Russian Platform] Pp. 65–223. *In* Grigelis, A. & Karatajūtė-Talimaa, V. (eds) *Voprosy geologii Litvy*. (Akademiya Nauk Litovskoy SSR, Institut Geologii i Geografii: Vilnius). [in Russian with Lithuanian, English summaries]

Long, J.A. 1991. The long history of fossil fish. Pp. 336–428. *In* Vickers-Rich, P., Monaghan, J.N., Baird, R.F. & Rich, T.H. (eds) *Vertebrate Palaeontology in Australasia*. (Pioneer Design Studio: Melbourne).

Lucševičs, E. 1991. *Remigolepis* (Pisces, Antiarchi) from the Famennian deposits of the Central Devonian Field. *Daba un muzejs* (Riga: Gandrs) **3**: 51–56. [in Russian with English abstract]

Lucševičs, E. 2001. The orbito-nasal area of *Asterolepis ornata*, a Middle Devonian placoderm fish. *Journal of Vertebrate Paleontology* **21**: 687–692. https://doi.org/10.1671/0272-4634(2001)021[0687:TONAOA]2.0.CO;2

Lyarskaya, L.A. 1981. *Placoderms from the Devonian of the Baltic region: Asterolepidae*. (Zinatne, Riga). [In Russian]

Moloshnikov, S.V. 2008. Devonian antiarchs (Pisces, Antiarchi) from central and Southern European Russia. *Paleontological Journal* **42**(7): 691–773. https://doi.org/10.1134/S0031030108070010

Newman, M., Den Blaauwen, J. & Leather, D. 2019. The antiarch fish *Asterolepis orcadensis* from the Scottish Middle Devonian. *Palaeontologia Electronica* **22.2.37A**: 1–24. https://doi.org/10.26879/970

Nilsson, T. 1941. The Downtonian and Devonian vertebrates of Spitzbergen. Order Antiarchi. *Skrifter om Svalbard og Ishavet* **82**: 1–54.

Pan, J., Huo, F.C., Cao, J.X., Gu, Q.C., Liu, S.Y., Wang, J.Q., Gao, L.D. & Liu, C. 1987. *Continental Devonian System of Ningxia and its Biotas*. (Geological Publishing House, Beijing).

Panteleyev, N. 1992. New remigolepids and high-armoured antiarchs of Kirgizia. Pp. 185-191. *In* Mark-Kurik, E. (ed.) *Fossil Fishes as Living Animals: Proceedings of the 2nd International Colloquium on the Middle Palaeozoic Fishes*. (Academia 1, Tallinn).

Ritchie, A. 2006. The great Devonian fish kill at Canowindra. Pp. 159-184. In Merrick, J.R., Archer, M., Hickey, G.M. & Lee, M.S.Y. (eds) *Evolution and Biogeography of Australasian Vertebrates*. (Auscipub Pty Ltd and Southwood Press: Sydney).

Ritchie, A., Wang, S.T., Young, G.C. & Zhang, G.R. 1992. The Sinolepidae, a family of antiarchs (placoderm fishes) from the Devonian of South China and eastern Australia. *Records of the Australian Museum* **44**(3): 319–370. https://doi.org/10.3853/j.0067-1975.44.1992.38

Säve-Söderbergh, G. 1932. Preliminary note on Devonian stegocephalians from East Greenland. *Meddelelser om Grønland* **98**(4): 1-211.

Smart, J. 1973. 1:250,000 Geological Series Explanatory notes, Gilberton Qld. Sheet E/54-16. 2nd ed.

Stensiö, E. 1931. Upper Devonian vertebrates from East Greenland, collected by the Danish Greenland expedition in 1929 and 1930. *Meddelelser om Grønland* **86**(1): 1–212.

Stensiö, E. 1948. On the Placodermi of the Upper Devonian of East Greenland. II. Antiarchi: subfamily Bothriolepinae. With an attempt at a revision of the previously described species of that subfamily. *Palaeozoologica Groenlandica* **2**: 5–622.

Stensiö, E.A. 1969. Elasmobranchiomorphi Placodermata Arthrodires. *In* Piveteau, J. (ed.) *Traité de Paléontologie*, **4**(2):71–692. (Masson: Paris).

Turner, S. 1982. A catalogue of fossil fish in Queensland. *Memoirs of the Queensland Museum* **20**: 599–611.

Turner, S., Basden, A. & Burrow, C.J. 2000. Devonian vertebrates of Queensland. *Courier Forschungsinstitut Senckenberg* **223**: 487–522.

White, D.A. 1959. New stratigraphic units in North Queensland geology. *Queensland Government Mining Journal* **60**: 442–447.

White, D.A. 1961. Geological history of the Cairns-Townsville hinterland, north Queensland. *BMR Report* **59**: 1–33.

White, D.A. 1962. 1:250,000 Geological Series Explanatory notes, Gilberton Qld. Sheet E/54-16.

White, D.A. 1965. The Geology of the Georgetown/Clarke River Area, Queensland. *BMR Bulletin* **71**: 1–165.

Withnall, I.W. & Hutton, L.J. 2013. North Australian craton. Pp. 23–112. *In* Jell, P.A. (ed.) *Geology of Queensland*. (Geological Survey of Queensland: Brisbane).

Withnall, I.W., Oversby, B.S., Bain, J.H.C. & Baker, E.M. 1980. Geology of the Gilberton 1:100 000 sheet area (7659), north Queensland. *BMR Record* **1980/002**: 167 p.

Wyatt, D.H. & Jell, J.S. 1980. Devonian and Carboniferous stratigraphy of the northern Tasman orogenic zone in the Townsville hinterland, North Queensland. Pp. 201–228. *In* Henderson, R.A. & Stephenson, P.J. (eds) *The Geology and Geophysics of Northeastern Australia*. (Geological Society of Australia, Queensland Division: Brisbane).

Young B., Dunstone R.L., Senden T.J. & Young G.C. 2013. A gigantic sarcopterygian (lobe-finned fish) from the Upper Devonian of south-eastern Australia (Eden, New South Wales). *PLoS ONE [Public Library of Science]* **8** (3), March 2013 e53871, pp. 1–30. https://doi.org/10.1371/journal.pone.0053871

Young, G.C. 1974. Stratigraphic occurrence of some placoderm fishes in the Middle and Late Devonian. *Newsletters on Stratigraphy*, **3**: 243–261. https://doi.org/10.1127/nos/3/1974/243

Young, G.C. 1983. A new antiarchan fish (Placodermi) from the Late Devonian of southeastern Australia. *BMR Journal* **8**: 71–81.

Young, G.C. 1984a. Reconstruction of the jaws and braincase in the Devonian placoderm fish *Bothriolepis*. *Palaeontology* **27**: 635–661.

Young, G.C. 1984b. An asterolepidoid antiarch (placoderm fish) from the Early Devonian of the Georgina Basin, central Australia, *Alcheringa* **8**: 65–80. https://doi.org/10.1080/03115518408619609

Young, G.C. 1987. Devonian fish remains from Billiluna, eastern Canning Basin, Western Australia. *BMR Journal of Australian Geology & Geophysics* **10**: 179–192.

Young, G.C. 1988. Antiarchs (placoderm fishes) from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Palaeontographica* A **202**: 1–125.

Young, G.C. 1990. New antiarchs (Devonian placoderm fishes) from Queensland, with comments on placoderm phylogeny and biogeography. *Memoirs of the Queensland Museum* **28**: 35–50.

Young, G.C. 1993. Middle Palaeozoic macrovertebrate biostratigraphy of eastern Gondwana. Chapter 9, pp. 208-251. In Long, J.A. (ed.) *Palaeozoic Vertebrate Biostratigraphy and Biogeography*. (Belhaven Press: London).

Young, G.C. 1996. Devonian (chart 4). Pp. 96-109. *In* Young, G.C. & Laurie, J.R. (eds) *An Australian Phanerozoic Timescale*. (Oxford University Press: Oxford).

Young, G.C. 1999. Preliminary report on the biostratigraphy of new placoderm discoveries in the Hervey Group (Upper Devonian) of central New South Wales. *Records of the Western Australian Museum, Supplement* **57**: 139–150.

Young, G.C. 2006. Devonian fish remains, biostratigraphy and unconformities, Narromine 1:250 000 sheet area, central New South Wales (Lachlan Fold Belt). *Australian Journal of Earth Sciences* **53**: 605–615. https://doi.org/10.1080/08120090600686769

Young, G.C. 2007. Devonian formations, vertebrate faunas, and age control on the far south coast of New South Wales and adjacent Victoria. *Australian Journal of Earth Sciences* **54**: 991–1008. https://doi.org/10.1080/08120090701488313

Young, G.C. 2008. The relationships of antiarchs (Devonian placoderm fishes) - evidence supporting placoderm monophyly. *Journal of Vertebrate Paleontology* **28**: 626–636. https://doi.org/10.1671/0272-4634(2008)28[626:TROADP]2.0.CO;2

Young, G.C. 2010a. Placoderms (Armored Fish): Dominant vertebrates of the Devonian Period. *Annual Review of Earth and Planetary Sciences* **38**(1): 523–550. https://doi.org/10.1146/annurev-earth-040809-152507

Young G.C. 2010b. A new antiarch (placoderm fish: Devonian) from the south coast of New South Wales, Australia. Pp. 85-100. *In* Elliott, D.K., Maisey J.G., Yu X., & Miao D. (eds) *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes* [in honor of Meemann Chang]. (Verlag Dr. Friedrich Pfeil: Munich).

Young, G.C. & Gorter, J.D. 1981. A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales. *BMR Bulletin* **209**: 83–147.

Young, G.C. & Lu J. 2020. Asia-Gondwana connections indicated by Devonian fishes from Australia: palaeogeographic considerations. *Journal of Palaeogeography* **9**: 8 pp. https://doi.org/10.1186/s42501-020-00057-x

Young, G.C. & Zhang, G.R. 1992. Structure and function of the pectoral joint and operculum in antiarchs, Devonian placoderm fishes. *Palaeontology* **35**: 443–464.

Young, G.C., Sherwin, L. & Raymond, O.L. 2000. Hervey Group. Pp. 125–149. *In* Lyons, P., Raymond, O.L. & Duggan, M.B. (eds) Forbes 1:250 000 Geological Sheet S155-7, 2nd edition, Explanatory Notes. *AGSO Record* **2000/20**, xviii + 230 pp.

Young, G.C., Burrow, C., Long, J.A., Turner, S., & Choo, B. 2010. Devonian macrovertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica). *Palaeoworld* **19**: 55–74. https://doi.org/10.1016/j.palwor.2009.11.005

Young, G.C., Dunstone, R.L., Ollerenshaw P.J., Lu, J. & Crook, B. 2019. New information on the giant Devonian lobe-finned fish *Edenopteron* from the New South Wales south coast. *Australian Journal of Earth Sciences* **67**: 221–242. https://doi.org/10.1080/08120099.2019.1651769

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A new carnivorous sponge (Porifera) from the Coral Sea

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ABSTRACT

A new species of carnivorous sponge, *Lycopodina coralseaensis* sp. nov., family Cladorhizidae, is described from the Louisiade Plateau, Coral Sea, off the east coast of Australia at bathyal depths of ~2000 m, collected during the RV *Investigator* 2019 voyage. The new species differs from other *Lycopodina* with stipitate morphology by lacking forceps microscleres, similar to *L. nikitawimandi* Ekins *et al.*, 2020a but differing in having only a very small single size class of palmate anisochelae, and most importantly by having a third category of mycalostyle echinating the stem and basal holdfast. This new species is the sixth *Lycopodina* recently described as new from the Australian Exclusive Economic Zone (*L. nikitawimandi, L. helios, L. cassida, L. brochidodroma* and *L. hystrix*), bringing the total number of carnivorous sponges known so far from Australia to 26.

❑ *Porifera, Cladorhizidae, Queensland, Tasmantid, seamounts, Lycopodina, new species.*

Carnivorous sponges (Cladorhizidae, Poecilosclerida) are unique amongst the Porifera, by having a reduced aquiferous system and an ability to capture and digest prey. They are predominantly a deep-water group living in bathyal to abyssal depths (Hestetun *et al.* 2017a) are are frequently found at oceanic ridges and seamount systems, with new species continuously discovered as new areas are explored. While they were first discovered in the mid 19th century, their diversity, taxonomy and geographic distributions are still poorly known due to their deep-sea life-style. However, recent advancements in technology have enabled greater exploration of these deep-sea habitats resulting in the recent escalation in the discovery of a much higher biodiversity than previously thought, leading new expeditions to discover many undescribed species - 23 of which were published in 2020 from Australasian waters alone (e.g. Ekins *et al.* 2020a, 2020b; Vacelet 2020).

The carnivorous sponge family Cladorhizidae Dendy, 1922 currently contains thirteen genera (*Abyssocladia* Lévi 1964, *Abyssosdiskos* Ekins *et al.* 2020b, *Asbestopluma* Topsent, 1901, *Axoniderma* Ridley & Dendy, 1886, *Bathytentacular* Ekins *et al.* 2020b, *Cercicladia* Rios *et al.*, 2011, *Chondrocladia* Thomson, 1873, *Cladorhiza* Sars, 1872, *Eucheliplum*a Topsent, 1909, *Koltunicladia* Hestetun *et al.*, 2016, *Lollipocladia* Vacelet 2008, *Lycopodina* Lundbeck, 1905 and *Nullarbora* Ekins *et al.*, 2020b) and five subgenera (*Asbestopluma (Asbestopluma)* Topsent, 1901, *Asbestopluma (Helophloeina)* Topsent, 1929, *Chondrocladia* (*Chondrocladia)* Thomson, 1873, *Chondrocladia* (*Meliiderma)* Ridley & Dendy, 1887 and

Chondrocladia (*Symmetrocladia)* Lee *et al.,* 2012), with 197 species described up to the present (Van Soest *et al.* 2020).

During August to September 2019, the RV *Investigator* (cruise IN2019_V04) mapped the seafloor and sampled the rocks and biology along the Tasmantid Seamounts, the Louisiade Plateau and Lord Howe Seamounts - one of the world's most extensive intraplate volcanic regions within the Coral Sea (Knesel *et al.* 2008; Richard *et al.* 2018). To date, this is only the second major expedition to sample the deep-sea biology of this general region between ~700 and ~3700 m depth, the first of which being the CIDARIS project from 1986 to 1992 (e.g. Pichon *et al.,* 1986). Specimens collected from the CIDARIS project are still being examined, leading to the descriptions of new species (e.g. Crowther *et al.* 2011), and range expansions of known species of other phyla to the region (e.g. Horowitz *et al.* 2018). A carnivorous sponge *Abyssocladia desmophora* (Hooper & Lévi, 1989) was discovered during the CIDARIS expeditions on the edge of the Australian continental shelf off Queensland at ~1200 m depth. More recently, another carnivorous sponge was found from within the Australian EEZ of the Coral Sea, *Chondrocladia* (*Chondrocladia*) *zygainadentonis* Ekins *et al.,* 2020a, from the edge of the continental shelf at ~1800 m depth. Other carnivorous species recorded from elsewhere in the Coral Sea include *Asbestopluma (Asbestopluma) biserialis* (Ridley & Dendy, 1886), from New Caledonia, *Cladorhiza similis* Ridley & Dendy, 1886, *Cladorhiza schistochela* Lévi, 1993, *Chondrocladia (Chondrocladia) pulvinata* Lévi 1993, *C.(C.) scolionema* Lévi, 1993 and most recently *Abyssocladia kanaconi* Vacelet, 2020, *A. microstrongylata* Vacelet, 2020 and *A. mucronata* Vacelet, 2020. For a list of descriptions including those from the east coast of Australia and the Pacific see Ekins *et al.* (2020a).

This present work describes another new species of Cladorhizidae, collected from the east coast of Australia during the 2019 research expedition of the *RV Investigator* to the Louisiade Plateau in the Coral Sea. The IN2019_V04 voyage collected 42 sponge specimens that have been deposited at the Queensland Museum, among which were three small Cladorhizidae (Figs 1-2). These samples build on recent contributions to the Australian cladorhizid fauna in which 17 new species were described from the east coast of Australia (Ekins *et al.* 2020a), and three new species from Great Australian Bight (Ekins *et al.* 2020b). The current list of species known so far from the Australian Exclusive Economic Zone (EEZ) are listed in Table 1.

MATERIALS AND METHODS

Collection methods. For details of collection methodology refer to Lucieer *et al.* (2020).

Morphological analysis. Scanning Electron Microscope (SEM) spicule preparations were made by dissolving the tissue in 12.5% sodium hypochlorite to remove the soft tissue, and neutralised in distilled water, rinsed twice in 70% ethanol and then finally rinsed twice in 98% ethanol and then air-dried. SEM preparations were sputter coated in gold to improve resolution. The scanning electron micrograph photos and measurements were made using a Hitachi TM-1000 SEM and plates assembled in Adobe Photoshop. Spicule dimensions were measured using SEM tools, and represented as minimum – (mean) – maximum lengths x widths of each spicule category. Nomenclatural acts proposed below are to be understood as authored by Merrick Ekins and John Hooper under ICZN Article 50.1 (ICZN, 1999).

RESULTS

SYSTEMATICS

Phylum PORIFERA Grant, 1836
Class DEMOSPONGIAE Sollas, 1885
Subclass HETEROSCLEROMORPHA
Cárdenas *et al.*, 2012
Order POECILOSCLERIDA Topsent, 1928a
Family CLADORHIZIDAE Dendy, 1922
Cladorhizeae Dendy, 1922:58
Cladorhizidae de Laubenfels, 1936:122.

Genus *Lycopodina* Lundbeck, 1905
Asbestopuma (*Lycopodina*) Lundbeck, 1905: 58.
Lycopodina Lundbeck, 1905: 58.
Cotylina Lundbeck, 1905: 68; de Laubenfels 1936: 122.

***Lycopodina coralseaensis* sp. nov.**
Ekins & Hooper
(Figs 3-4, Tables 1-2)
urn:lsid:zoobank.org:act:2EE2E9CB-F246-4202-8AAE-F68F868B1E5A)

Material Examined. Holotype: QM G339172, Louisiade Plateau, Coral Sea, Australia, IN2019_V04_30, 14°26.6′ S, 155°48.32′ E - 14°27.07′ S, 155°48.5′ E, 1954-2814 m, Rock Dredge, Coll. Jeremy Horowitz, CSIRO on RV Investigator, Cruise IN2019_V04, Sample iv89, 20/VIII/2019. Paratype: QM G339173 same collection data as QM G339172, Sample iv90, 20/VIII/2019. Paratype: QM G339215 same collection data as QM G339172, Sample iv89.

Distribution. Known so far only from the Louisiade Plateau, Coral Sea, Australia, at bathyal depths.

Etymology. *Coralseaensis,* named after the Coral Sea type locality.

DESCRIPTION

Growth form. Erect stipitate, arbuscular, clavate-shaped body, with a very hispid array of filaments arising at all angles from the body, supported by a long stem and a globular basal attachment (Fig. 3A). The holotype, QM G339172, is 8 mm in total length, with the sponge body 4 mm in length and 1.5 mm in diameter including the projecting filaments. Paratype QM G339173 has a total length of 9.6 mm, with the body only 4.3 mm in length, and 1.8 mm in width. Paratype QM G339215 has a total length of 26.2 mm, body 5 mm wide, 11.8 mm long (Fig. 3B).

Colour. Alive on-deck the body, stem, basal disc and base of the filaments were cream. After preservation in ethanol the sponges retained their cream colouration.

Ectosomal skeleton. A thin membranous ectosome covers the sponge with anisochelae embedded in the outer surface of the ectosome, including the terminal end of the basal attachment.

Choanosomal skeleton. The skeleton consists of several bundles of the larger mycalostyles 1 forming the longitudinal axis extending from the base of the stem to the top of the sponge body (Figs. 3 D-E, 4C). At right angles to the axial core are bundles of medium sized mycalostyles 2 forming bouquets along the length of these tracts (Figs 3F-G, 4B). The stem and basal attachment of the sponge is echinated by the smaller subtylote mycalostyles 3 (Figs 3H-I, 4C-D).

Megascleres. Megascleres consist of three categories of mycalostyles-tylostyles. Mycalostyles 1 of the body and stem are oxeote, having a long tapering point and a tapering rounded basal end, with the thickest part of the spicule approximately in the middle (Fig. 3D-E, Table 2). Dimensions: 507-2820 x 15-45 µm. The medium sized mycalostyles 2 that form the echinating bouquets tangential to the axial skeleton of the body are styles tending towards subtylostyles, with only a slight constriction near or at the basal end, and thickest diameter between the middle and one third towards the base (Fig. 3 F-G). Dimensions: 217-691 x 3-15 µm. The smaller basal styles 3 that echinate the stem and basal attachment are styles or only faintly subtylostyles, with their thickest diameter at the basal end (Fig. 3H-I, Table 2). Dimensions: 69-212 x 2-6 µm.

Microscleres. The microscleres consist only of a single size class of palmate anisochelae (Fig. 3C, Table 2). Dimensions 5.8-10.9 x 2.0-6.3 µm. Forceps found in the majority of other species of *Lycopodina* were absent in all three specimens known so far for this new species. The anisochelae have a single upper large frontal alae nearly completely detached from the two lateral alae which are completely fused to the fimbria, and two smaller lower alae nearly completely fused. The lower alae also has a central dominant tooth with three blunt terminal spines, and the other small alae directly behind it has four blunt teeth, arranged in pairs of unequal sizes.

Remarks. This new species shares similar stipitate morphology with ten other *Lycopodina* species (*L. nikitawimandi* Ekins *et al.*, 2020a, *L. brochidodroma* Ekins *et al.*, 2020a, *L. drakensis* Goodwin *et al.*, 2017, *L. hystrix* Ekins *et al.*, 2020b, *L. lycopodium* (Levinsen 1887), *L. microstrongyla* (Lopes *et al.*, 2011), *L. novangliae* Hestetun *et al.*, 2017b, *L. occidentalis* (Lambe, 1893), *L. tendali* Hestetun *et al.*, 2017b and *L. vaceleti* (Van Soest & Baker 2011); see Table 14 in Ekins *et al.* 2020a). However, *L. coralseaensis* sp. nov. differs from

Table 1. Inventory of known Cladorhizidae species recorded from the Australian EEZ

Genus	Species	Distribution	Source
Abyssocladia	*annae* Ekins, Erpenbeck & Hooper, 2020	continental shelf of central New South Wales, Tasman Sea; abyssal	Ekins *et al.* 2020a: 23-25, Fig. 4
	desmophora (Hooper & Lévi, 1989)	continental slope off Townsville, Coral Sea, Queensland; bathyal	Hooper & Lévi 1989: 437-440, Figs 1-4
	escheri Ekins, Erpenbeck & Hooper, 2020	off Fraser Island, Queensland, Coral Sea; abyssal	Ekins *et al.* 2020a: 8,21-23, Fig. 2
	gliscofila Ekins, Erpenbeck & Hooper, 2020	continental shelf adjacent to the Hunter Valley Region, Tasman Sea, New South Wales, and off the Gold Coast, Coral Sea, Queensland; bathyal	Ekins *et al.* 2020a: 25-28, Fig. 5
	oxyasters Ekins, Erpenbeck, Goudie & Hooper, 2020	Nullarbor Canyon, Great Australian Bight, South Australia, Southern Ocean; bathyal	Ekins *et al.* 2020b: 247-251, Figs 4-6
Abyssosdiskos	*pentaeiros* (Ekins, Erpenbeck & Hooper, 2020)	off Bermagui, New South Wales, Tasman Sea; bathyal	Ekins *et al.* 2020a: 86-88, Fig. 17
Asbestopluma (Asbestopluma)	*desmophora* Kelly & Vacelet, 2011	seamounts on the Macquarie Ridge between Australia and New Zealand, Southwest Pacific; mesophotic-bathyal	Kelly & Vacelet 2011: 62-67, Figs 5-6
	maxisigma Ekins, Erpenbeck & Hooper, 2020	continental slope off Jervis Bay, New South Wales, Tasman Sea; bathyal	Ekins *et al.* 2020a: 28-29, 46, Fig. 6
Axoniderma	*australis* (Ekins, Erpenbeck & Hooper, 2020)	off Tasmania and New South Wales, Tasman Sea; abyssal	Ekins *et al.* 2020a: 47-49, 72, Figs 7-8
	poritea (Ekins, Erpenbeck & Hooper, 2020)	off Fraser Island, Coral Sea, Queensland, and Freycinet Peninsula, Tasman Sea, Tasmania; abyssal	Ekins *et al.* 2020a: 72-75, Figs 9-10
Bathytentacular	*moniqueae* (Ekins, Erpenbeck & Hooper, 2020)	off Newcastle, New South Wales, Tasman Sea; abyssal	Ekins *et al.* 2020a: 82-85, Figs 14-15
Chondrocladia (Meliiderma)	*tasmaniensis* Vacelet, Kelly & Schlacher-Hoenlinger, 2009	seamounts south of Tasmania, Tasman Sea; bathyal	Vacelet *et al.* 2009: 63-65, Fig. 4
Chondrocladia (Chondrocladia)	*callistemonex* Ekins, Erpenbeck & Hooper, 2020	off Newcastle, New South Wales, Tasman Sea; abyssal	Ekins *et al.* 2020a: 117-120, Figs 22-23
	clavata Ridley & Dendy, 1886	Fiji, Antarctica, Madagascar, New Zealand, and New South Wales, Tasman Sea; bathyal	Ridley & Dendy 1886:345; Ridley & Dendy 1887: 100, Pl. XX, Figs. 1, 1a, Pl. XXI, Fig. 11; Ekins *et al.* 2020a: 89-114, Figs 18-19
	freycinetensis Ekins, Erpenbeck & Hooper, 2020	off the Freycinet Peninsula, Tasmania, and Jervis Bay, New South Wales, Tasman Sea; bathyal	Ekins *et al.* 2020a: 114-117, Figs 20-21
	zygainadentonis Ekins, Erpenbeck & Hooper, 2020	off Gladstone, Coral Sea, Queensland; bathyal	Ekins *et al.* 2020a:120-123, Figs 24-25
Euchelipluma	*claudochela* Ekins, Erpenbeck & Hooper, 2020	off Central New South Wales, Tasman Sea; abyssal	Ekins *et al.* 2020a: 149-153, Fig. 32
Lycopodina	*brochidodroma* Ekins, Erpenbeck & Hooper, 2020	off Moreton Island, Coral Sea, Queensland; abyssal	Ekins *et al.* 2020a: 148-149, Fig. 31
	calyx Hentschel, 1914	Kaiser Wilhelm Land, Antarctica; Southern and central Eastern Australia, New South Wales and Victoria Tasman Sea; bathyal-abyssal	Hentschel 1914: 66, Pl. IV, Fig. 4, Pl. V, Fig. 11; Ekins *et al.* 2020a: 123-124, 140-141, Fig. 26
	cassida Ekins, Erpenbeck & Hooper, 2020	off Fraser Island, Coral Sea, Queensland; bathyal	Ekins *et al.* 2020a: 146-147, Fig. 30
	helios Ekins, Erpenbeck & Hooper, 2020	off Cape Barren Island, Flinders Central Marine Reserve, Tasman Sea, Tasmania	Ekins *et al.* 2020a: 144-146, Fig. 29
	hystrix Ekins, Erpenbeck, Goudie & Hooper, 2020	Yatala Canyon, Great Australian Bight, South Australia, Southern Ocean; bathyal	Ekins *et al.* 2020b: 252-254, Fig. 7
	nikitawimandi Ekins, Erpenbeck & Hooper, 2020	Central East coast and central Tasmania, Tasman Sea; bathyal-abyssal	Ekins *et al.* 2020a: 141-144, Figs 27-28
	coralseaensis sp. nov.	Louisiade Plateau, Coral Sea, Queensland; bathyal	Present study
Nullarbora	*investigator* (Ekins, Erpenbeck & Hooper, 2020)	off the Freycinet Peninsula, Tasman Sea, Tasmania; bathyal	Ekins *et al.* 2020a: 78-82, Figs 12-13
	heptaxia (Ekins, Erpenbeck, Goudie & Hooper, 2020)	Nullarbor Canyon, Great Australian Bight, South Australia, Southern Ocean; bathyal	Ekins *et al.* 2020b: 244-247, Figs 1-3

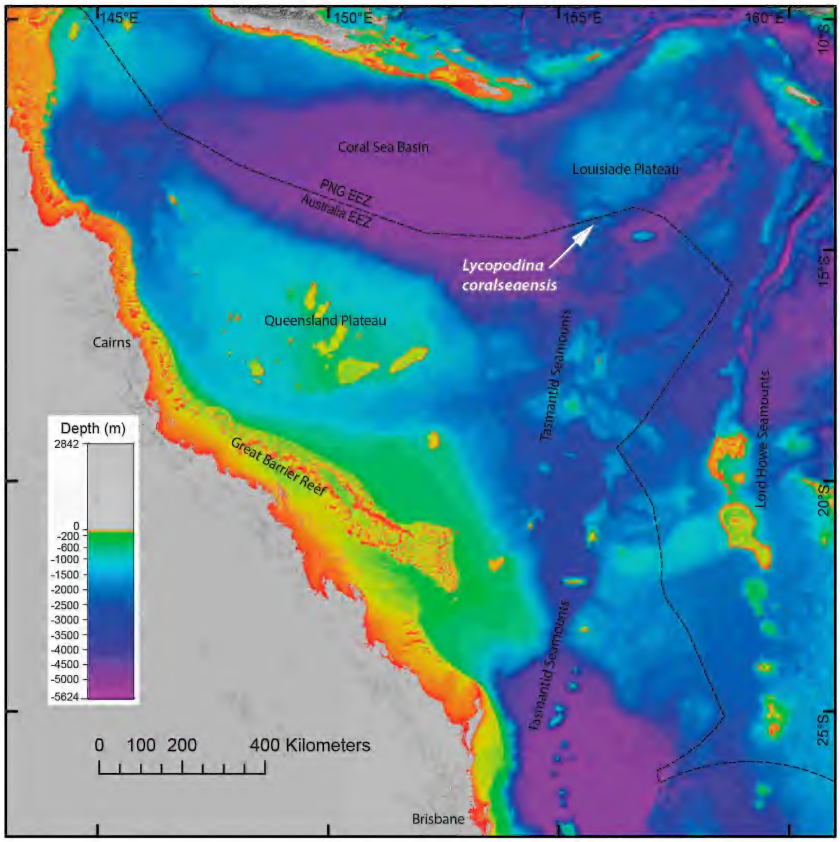

FIG. 1. Location of the *Lycopodina coralseaensis* sp. nov. in the Louisiade Plateau in the Coral Sea.

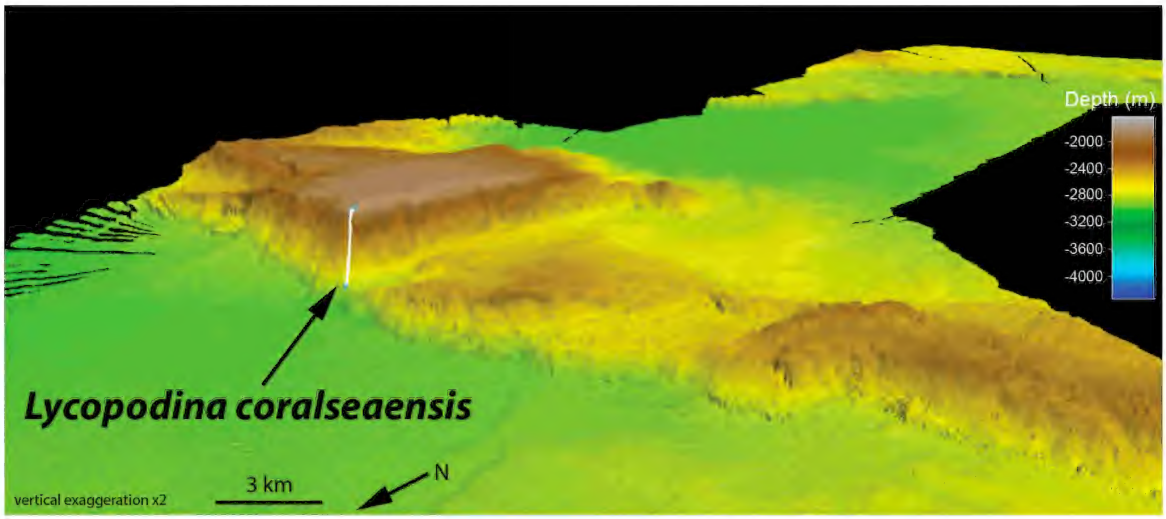

FIG. 2. A 3D view of the dredge 30 site at the crest of a ridge on the Louisiade Plateau, from which all the samples of *Lycopodina coralseaensis* sp. nov. were collected.

	Mycalostyle 1	Mycalostyle 2	Basal style	Anisochelae	Large basal style	Basal tylostyle	Basal strongyles	Forceps	Sigmancistra
Lycopodina coralseansis sp. nov. Holotype QM G337172	507-(954)-1430 x 14.5-(26.0)-36.0, *n*=21	262-(426)-691 x 4.0-(6.9)-9.7, *n*=53	69-(126)-212 x 2.1-(3.8)-6.0, *n*=52	5.8-(8.4)-9.9 x 2.0-(3.8)-5.6, *n*=73 Large alae 2.1-(2.7)-4.9, Small alae 1.3-(2.1)-2.7, *n*=25	Absent	Absent	Absent	Absent	Absent
Lycopodina coralseansis sp. nov. Paratype QM G337173	741-(989)-1320 x 19.4-(25.8)-35.0, *n*=11	217-(434)-581 x 3.4-(7.6)-14.5, *n*=62	69-(126)-159 x 2.0-(3.3)-4.6, *n*=40	6.9-(8.6)-10.0 x 3.1-(4.2)-5.1, *n*=49 Large alae 1.9-(2.4)-3.2, Small alae 1.3-(2.0)-2.8, *n*=17	Absent	Absent	Absent	Absent	Absent
Lycopodina coralseansis sp. nov. Paratype QM G337215	563-(1453)-2820 x 15.1-(32.2)-44.7, *n*=20	276-(399)-565 x 5.6-(9.2)-14.9, *n*=53	98-(141)-188 x 1.7-(3.4)-5.3, *n*=51	7.1-(9.4)-10.9 x 3.0-(4.6)-6.3, *n*=52 Large alae 2.1-(2.8)-3.5, Small alae 1.6-(2.2)-2.7, *n*=24	Absent	Absent	Absent	Absent	Absent
Lycopodina nikitawimandi Ekins *et al.*, 2020a (mean of all types)	1040-(1449)-1910 x 12-(22)-37, *n*=186	209-(577)-992 x 3-(11)-19, *n*=338	Absent	10.4-(14.3)-17.8 x 2.8-(3.9)-6.0, *n=312* Large alae 2-6 Small alae 3-4	Absent	Absent	Absent	Absent	Absent
Lycopodina hystrix Ekins *et al.*, 2020b (mean of all types)	496-(1145)-2170 x 4-(17)-28, *n*=109	107-(168)-258 x 3-(6)-9, *n*=76	106-(215)-322 x 4-(7)-12, *n*=93	*10.5-(13.1)-16.1 x 5.0-(6.2)-8.0, n=267* Large alae 2.6-(3.9)-5.0 Small alae 2.0-(2.6)-3.4 *n*=135	348-(547)-1480 x 3.6-(8.7)-18.5, *n*=51	107-(168)-258 x 2.9-(6.2)-9.1, *n*=76	36-(59)-81 x 3.3-(5.1)-6.7, *n*=44	15.5-(41.6)-50.8 x 3.3-(7.6)-11.4, *n*=26	7.7-(10.2)-12.6 x 0.4-(0.8)-1.3, *n*=16

TABLE 2. A comparison of spicule measurements (µm) between the different specimens of *Lycopodina coralseaensis* sp. nov. and comparison of spicule dimension with its sister species *L. nikitawimandi* from the east coasts of New South Wales and Tasmania (Ekins *et al.* 2020a) and *L. hystrix* from South Australia (Ekins *et al.* 2020b).

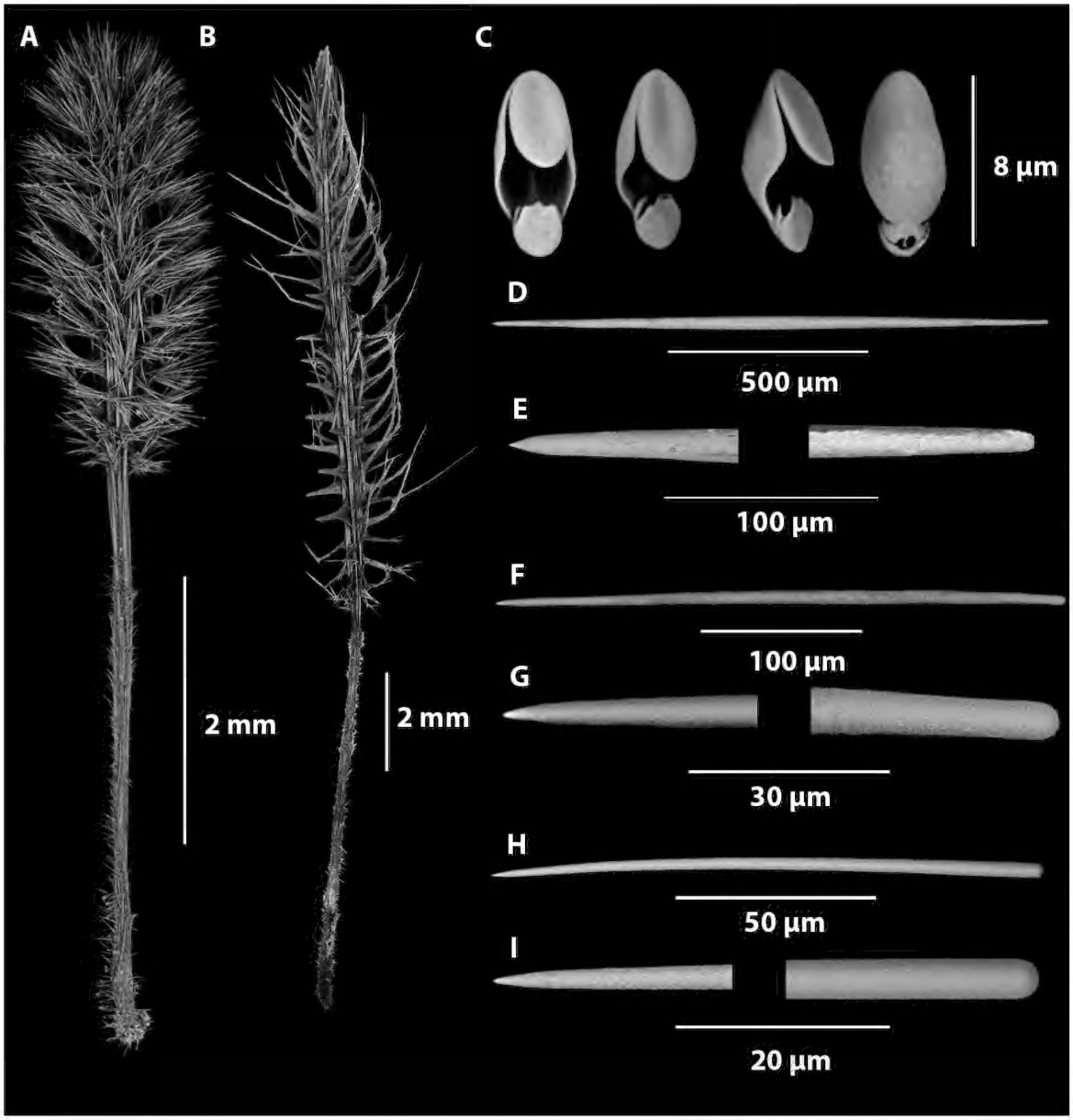

FIG. 3. *Lycopodina coralseaensis* sp. nov. **A**, Holotype QM G339172; **B**, Paratype QM G339215; **C**, Abyssochelae; **D**, Larger mycalostyle 1 that forms axial skeletal tracts in both the stem and body; **E**, Magnified ends of the mycalostyle 1 depicted in D; **F**, Medium sized mycalostyle 2 from the body; **G**, Magnified ends of the mycalostyle 2 depicted in F; **H**, Smaller basal style 3 echinating the stem; **I**, Magnified ends of the basal style 3 depicted in H.

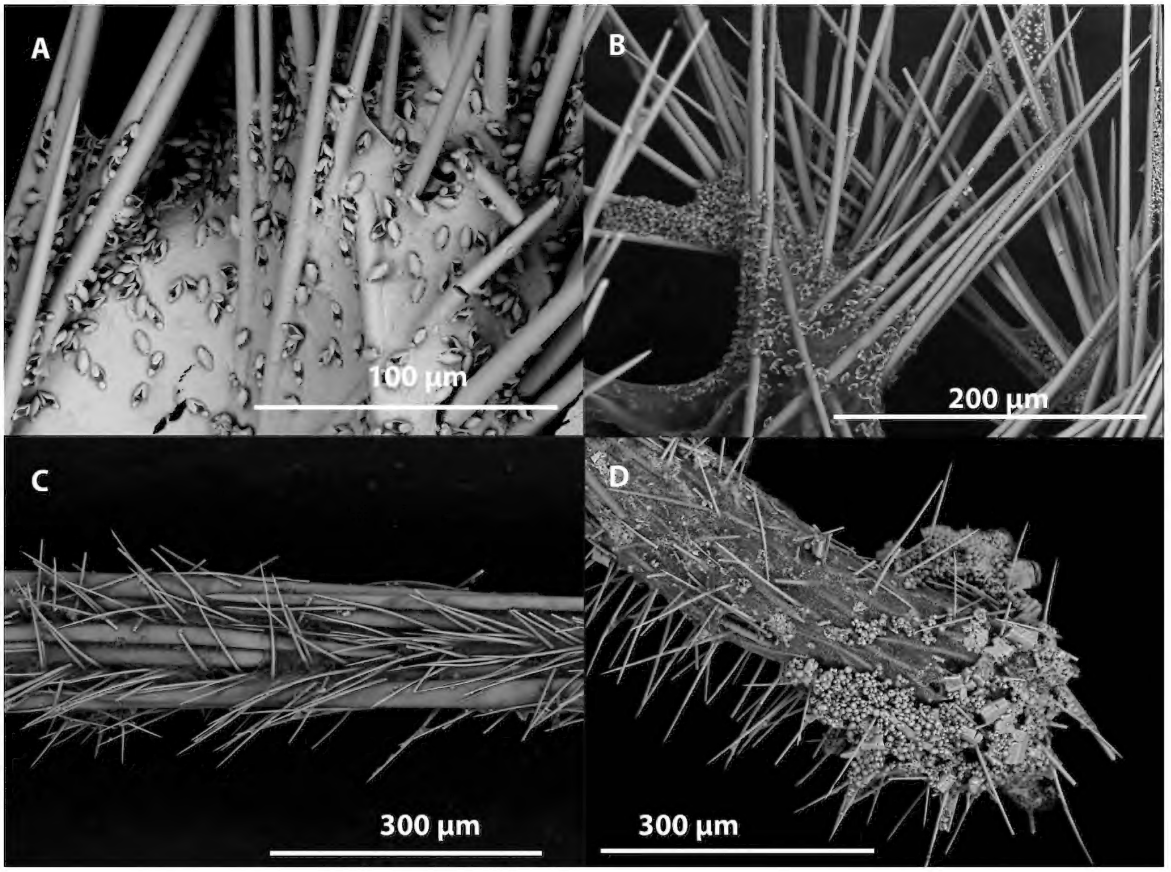

FIG. 4. *Lycopodina coralseaensis* sp. nov. **A**, Close-up of the sponge body, showing the embedded mycalostyles 2 forming erect bouquets projecting from the surface, and the anisochelae embedded on the thin ectosome; **B**, Mycalostyles 2 projecting from the longitudinal tracts of mycalostyles 1 in the sponge body, and anisochelae encrusting the soft tissue surrounding those tracts; **C**, Stem of the sponge showing the large tracts of mycalostyles 1 forming the axial skeleton of the stem, and the smaller mycalostyles 3 echinating those tracts; **D**, The slightly globular basal attachment with echinating mycalostyles 3 and soft tissue encrusted by anisochelae at its termination.

nine of these stipitate species in lacking forceps microscleres. Forceps however, appear to be associated with sexually reproducing individuals (e.g. Riesgo *et al.* 2007) and are often rare or absent. This new species is similar in this regard to *L. nikitawimandi* from bathyal-abyssal depths off the east coasts of New South Wales and Tasmania, from which it differs in having only a very small single size class of palmate anisochelae and a third category of mycalostyle echinating the axis of the stem and basal holdfast. *Lycopodina hystrix* from Southern Australia has a much larger palmate anisochelae, forceps and at least two extra classes of styles.

DISCUSSION

With the discovery of *Lycopodina coralseaensis* sp. nov. from bathyal depths on the Louisiade Plateau, lying north of the Tasmantid Seamounts off Queensland, Australia, the present study brings the total number of cladorhizid carnivorous sponges described from Australia's Exclusive Economic Zone to 26 species in 9 genera, occurring from deep mesophotic to

abyssal depths (Table 1). This species has morphological similarities to two other species, occurring around Australia i.e. *L. nikitawimandi* and *L. hystrix*. Due to the minute size of these sponges, they can easily be overlooked during sampling of deep-sea rocks using dredges, where the main focus is geological sampling. It is only due to the presence of the biologists on board who were able to secure these fragile carnivores of the deep. To date, only three samples of this new species have been recovered, and all three were used in the manufacture of SEM stubs. Future explorations, including the use of remote operated vehicles, will determine if the distributions of these rare species are restricted to particular seamounts or plateaus, or have more widespread distribution across the oceans. In this case, all three samples were collected from the same rock dredge. Some carnivorous species have wide distributions, such as *Chondrocladia (Chondrocladia) clavata* Ridley & Dendy, 1886, found on the continental slopes of Fiji (Ridley & Dendy 1887), Australia (Ekins *et al.* 2020a), Antarctica (Dressler-Allame *et al.* 2017) and Madagascar (Lévi 1964), and *Lycopodina calyx* (Hentschel, 1914) found in Antarctica (Goodwin *et al.* 2017) and Australia (Ekins *et al.* 2020a). Like many known sponge species, the majority of carnivorous sponges have been recovered only once. Molecular results in the future may discover whether the widespread species such as *C. (C.) clavata* are genetically separated. But because of the higher than expected gene flow that occurs in deep sea sponges (Ekins *et al.* 2015), perhaps the bathyal and abyssal carnivorous fauna are all more connected than we presently assume.

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LITERATURE CITED

Cárdenas, P., Pérez, T. & Boury-Esnault, N. 2012. Chapter 2. Sponge Systematics Facing New Challenges. *Advances in Marine Biology*. **61**, 79–209. https://doi.org/10.1016/B978-0-12-387787-1.00010-6

Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*. **17**(4), 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Chombard, C., Boury-Esnault, N. & Tillier, S. 1998. Reassessment of homology of morphological characters in tetractinellid sponges based on molecular data. *Systematic Biology*. **47**, 351–366. https://doi.org/10.1080/106351598260761

Crowther, A.L., Fautin, D.G., & Wallace, C.C. 2011. *Stylobates birtlesi* sp. n., a new species of carcinoecium forming sea anemone (Cnidaria, Actiniaria, Actiniidae) from eastern Australia. *ZooKeys*, **89**, 33–48. https://doi.org/10.3897/zookeys.89.825

de Laubenfels, M.W. 1936. A Discussion of the Sponge Fauna of the Dry Tortugas in Particular and the West Indies in General, with Material for a Revision of the Families and Orders of the Porifera. *In*: Carnegie Institute of Washington Publication 467. *Tortugas Laboratory Paper*. 30, pp. 1–225, pls. 1–22.

Dendy, A. 1922. Report on the Sigmatotetraxonida collected by H.M.S. '*Sealark*' in the Indian Ocean. *In*: Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905. Vol. 7. *Transactions of the Linnean Society of London*. **18** (1), pp. 1–164, pls. 1–18. https://doi.org/10.1111/j.1096-3642.1922.tb00547.x

Dressler-Allame, M., Göcke, C., Kersken, D., Plotkin, A. & Janussen, D. 2017. Carnivorous sponges (Cladorhizidae) of the deep Weddell Sea, with description of two new species. *Deep-Sea Research II*. **4121**, 190-206. https://doi.org/10.1016/j.dsr2.2016.08.006

Ekins, M., Erpenbeck, D. Wörheide, G. & Hooper, J.N.A. 2015. Staying well connected – Lithistid sponges on seamounts. *Journal of the Marine Biological Association of the United Kingdom*. **96**(2), 437-451. http://dx.doi.org/10.1017/S0025315415000831.

Ekins, M., Erpenbeck, D. & Hooper, J.N.A. 2020a. Carnivorous sponges from the Australian Bathyal and Abyssal zones collected during the RV Investigator 2017 Expedition. Zootaxa. **4774**(1), 1-159. https://doi.org/10.11646/zootaxa.4774.1.1

Ekins, M., Erpenbeck, D., Goudie, L. & Hooper, J.N.A. 2020b. New carnivorous sponges and allied species from the Great Australian

Bight. *Zootaxa*. **4878**(2), 240-246. https://doi.org/10.11646/zootaxa.4878.2.2

Erpenbeck, D., Ekins, M., Enghuber, N., Hooper, J.N.A., Lehnert, H., Poliseno, A., Schuster, A., Setiawan, E., de Voogd, N.J., Wörheide, G. & van Soest, R.W.M. 2016. Nothing in (sponge) biology makes sense – except when based on holotypes. *Journal of the Marine Biological Association of the United Kingdom*. **96**, 305–311 https://doi.org/10.1017/S0025315415000521

Goodwin, C.E., Berman, J., Downey, R.V. & Hendry, K.R. 2017. Carnivorous sponges (Porifera: Demospongiae: Poecilosclerida: Cladorhizidae) from the Drake Passage (Southern Ocean) with a description of eight new species and a review of the family Cladorhizidae in the Southern Ocean. *Invertebrate Systematics*. **31**(1), 37–64. https://doi.org/10.1071/IS16020

Grant, R.E. 1836. Animal Kingdom. *In*: Todd, R.B. (Ed.), *The Cyclopaedia of Anatomy and Physiology*. Vol. 1. Sherwood, Gilbert, and Piper, London, pp. 107–118.

Hentschel, E. 1914. Monaxone Kieselschwämme und Hornschwämme der Deutschen Südpolar-Expedition 1901–1903. *Deutsche Südpolar-Expedition*. **15**(1), 35–141, pls. IV–VIII.

Hestetun, J.T., Vacelet, J., Boury-Esnault, N., Borchiellini, C., Kelly, M., Ríos, P., Cristobo, F.J. & Rapp, H.T. 2016. The systematics of carnivorous sponges. *Molecular Phylogenetics & Evolution*. **94**, 327–345. https://doi.org/10.1016/j.ympev.2015.08.022

Hestetun, J.T., Rapp, H.T. & Xavier, J. 2017a. Carnivorous sponges (Porifera, Cladorhizidae) from the Southwest Indian Ocean Ridge seamounts. *Deep Sea Research Part II: Topical Studies in Oceanography*. **137**, 166–189. https://doi.org/10.1016/j.dsr2.2016.03.004

Hestetun, J.T., Tompkins-Macdonald, G. & Rapp, H.T. 2017b. A review of carnivorous sponges (Porifera: Cladorhizidae) from the boreal north Atlantic and Arctic. *Zoological Journal of the Linnaean Society*. **181**, 1–69. https://doi.org.10.1093/zoolinnean/zlw022

Hooper, J.N.A. & Lévi, C. 1989. *Esperiopsis desmophora* n. sp. (Porifera: Demospongiae): a desma-bearing Poecilosclerida. *Memoirs of the Queensland Museum*. **27**(2), 437–441.

Horowitz, J., Opresko, D. M., & Bridge, T.C.L. 2018. Black corals (Anthozoa: Antipatharia) from the deep (916 m–2542 m) Coral Sea, north-eastern Australia. *Zootaxa*, **4472**(2), 307. https://doi.org/10.11646/zootaxa.4472.2.5

International Commision of Zoological Nomenclature (ICZN) 1999. International Code of Zoological Nomenclature. The International Trust for Zoological Nomenclature. 4th Edition. http://iczn.org/iczn/index.jsp

Kelly, M. & Vacelet, J. 2011. Three new remarkable carnivorous sponges (Porifera, Cladorhizidae) from deep New Zealand and Australian (Macquarie Island) waters. *Zootaxa*. **2976** (1), 55–68. https://doi.org/10.11646/zootaxa.2976.1.4

Knesel, K.M., Cohen, B.E., Vasconcelos, P.M., Thiede, D.S. 2008. Rapid change in drift of the Australian plate records collision with Ontong Java plateau. *Nature*. **454**, 754-758. https://doi: 10.1038/nature07138

Lambe, L.M. 1893 [1894]. Sponges from the Pacific coast of Canada. *Proceedings and Transactions of the Royal Society of Canada*. **11** (4), 25–43, pls. II–IV.

Lee, W.L., Reiswig, H.M., Austin, W.C. & Lundsten, L. 2012. An extraordinary new carnivorous sponge, *Chondrocladia lyra*, in the new subgenus *Symmetrocladia* (Demospongiae, Cladorhizidae), from off of northern California, USA. *Invertebrate Biology*. **131** (4), 259–284. https://doi.org/10.1111/ivb.12001

Lévi, C. 1964. Spongiaires des zones bathyale, abyssale et hadale. *Galathea Report. Scientific Results of The Danish Deep-Sea Expedition Round the World, 1950–52*. **7**, 63–112.

Lévi, C. 1993. Porifera Demospongiae: Spongiaires bathyaux de Nouvelle-Calédonie, récoltés par le 'Jean Charcot' Campagne BIOCAL, 1985. In: A. Crosnier (ed.) *Résultats des Campagnes MUSORSTOM*, Volume 11. *Mémoires du Muséum national d'Histoire naturelle, (A)* **158**, 9-87.

Levinsen, G.M.R. 1887. Kara-Havets Svampe (Porifera). *Dijmphna-Togtets zoologisk- botaniske Udbytte*. **1**, 339–372, pls. XXIX–XXXI.

Lopes, D.A., Bravo, A. & Hajdu, E. 2011. New carnivorous sponges (Cladorhizidae: Poecilosclerida: Demospongiae) from off Diego Ramirez Archipelago (south Chile), with comments on taxonomy and biogeography of the family. *Invertebrate Systematics*. **25**, 407–443. https://doi.org/10.1071/IS11015

Lucieer, V., Beamn, R., Woehler, E., Horowitz, J., Nau, A. & Vandenbossche, P. 2020. Post survey report for the Coral Sea Australian Marine Park. Milestone Report #12. Report to the National Environmental Science Program, Marine Biodiversity Hub. University of Tasmania. 68 pp.

Lundbeck, W. 1905. Porifera. (Part II.) Desmacidonidae (pars.). *In*: *The Danish Ingolf-Expedition*. **6**(2). Bianco Luno, Copenhagen, pp. 1–219, pls. I–XX.

Pichon, M., Arnold, P.W. & Birtles, R.A. 1986. The deep sea bottom fauna of the Barrier Reef and adjacent Coral Sea. Cruise Summary, R.V. '*Franklin*', FR 3/86. CSIRO. 6 pp.

Richards, F.D., Kalnins, L.M., Watts, A.B., Cohen, B.E., Beaman, R.J. 2018. The morphology of the Tasmantid Seamounts: Interactions between tectonic inheritance and magmatic evolution.

Geochemistry, Geophysics, Geosystems. **19**(10), 3870-3891. https://doi: 10.1029/2018GC007821

Ridley, S.O. & Dendy, A. 1886. Preliminary report on the Monaxonida collected by H.M.S. *Challenger*. Part I. *Annals and Magazine of Natural History*. **18**, 325–351 + 470–493. https://doi.org/10.1080/00222938609459998

Ridley, S.O. & Dendy, A. 1887. Report on the Monaxonida collected by H.M.S. *Challenger* during the years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. 'Challenger', 1873–1876*, Zoology. **20**(59), i–lxviii + 1–275, pls. I–LI, 1 map.

Riesgo A., Taylor, C. & Leys, S.P. 2007. Reproduction in a carnivorous sponge: the significance of the absence of an aquiferous system to the sponge body plan. *Evolution & Development.* **9,** 618–631. https://doi.org/10.1111/j.1525-142X.2007.00200.x

Ríos, P., Kelly, M. & Vacelet, J. 2011. *Cercicladia australis*, a new carnivorous sponge with novel chelae from the Tasman Basin and the Argentine Patagonian Margin (Porifera, Cladorhizidae). *Zootaxa.* **3131**(1), 52–62. https://doi.org/10.11646/zootaxa.3131.1.3

Sars, G.O. 1872. Spongiae. *In*: Kongelige Norske Universitet (Ed.), *On some remarkable forms of animal life from the great depths off the Norwegian coast. I. Partly from posthumous manuscripts of the late professor Dr. Michael Sars.* Brøgger & Christie, Christiania, pp. 1–82, pls. I–VI., pp. 62–82, pl. VI.

Sollas, W.J. 1885. A Classification of the Sponges. *Annals and Magazine of Natural History*. Series 5, **16**(95), 395. https://doi.org/10.1080/00222938509459901

Thomson, C.W. 1873. *The Depths of the Sea*. Macmillan and Co., London, 527 pp.

Topsent, E. 1901. Spongiaires. Résultats du voyage du S.Y. 'Belgica' en 1897–99 sous le commandement de A. de Gerlache de Gomery. *Expédition antarctique belge. Zoologie*. **4**, 1–54, pls. I–VI. https://doi.org/10.5962/bhl.part.18721

Topsent, E. 1909. Etude sur quelques *Cladorhiza* et sur *Eucheliplumа pristina* n. g. et n. sp. *Bulletin de l'Institut océanographique, Monaco*. **151**, 1–23, pls. I–II.

Topsent, E. 1928a. Spongiaires de l'Atlantique et de la Méditerranée provenant des croisières du Prince Albert ler de Monaco. *Résultats des campagnes scientifiques accomplies par le Prince Albert I. Monaco*. **74**, 1–376, pls. I–XI.

Topsent, E. 1929. Notes sur *Helophloeina stylivarians* n.g. n.sp., Mycaline à desmes des Canaries. *Bulletin de l'Institut Océanographique, Monaco*. **533**, 1–8.

Vacelet, J. 2008. A new genus of carnivorous sponges (Porifera: Poecilosclerida, Cladorhizidae) from the deep N-E Pacific, and remarks on the genus *Neocladia. Zootaxa*. **1752**(1), 57–65. https://doi.org/10.11646/zootaxa.1752.1.3

Vacelet, J. 2020. Carnivorous sponges (Porifera, Cladorhizidae) from the deep South Pacific (New Caledonia) with the description of three new species of the genus *Abyssocladia* and remarks on genus *Cercicladia. Zootaxa.* **4767**(2), 257-276 https://doi.org/10.11646/zootaxa.4767.2.3

Vacelet, J., Kelly, M. & Schlacher-Hoenlinger, M. 2009. Two new species of *Chondrocladia* (Demospongiae: Cladorhizidae) with a new spicule type from the deep south Pacific, and a discussion of the genus *Meliiderma. Zootaxa.* **2073**(1), 57–68. https://doi.org/10.11646/zootaxa.2073.1.5

Van Soest, R.W.M. & Baker, B.J. 2011. A new carnivorous shallow-water sponge from McMurdo Sound, Antarctica (Porifera, Poecilosclerida). *Marine Biodiversity*. **41**(4), 495-501. https://doi.org/10.1007/s12526-010-0076-6

Van Soest, R.W.M., Boury-Esnault, N., Hooper, J.N.A., Rützler, K., de Voogd, N.J., Alvarez, B., Hajdu, E., Pisera, A.B., Manconi, R., Schönberg, C., Klautau, M., Kelly, M., Vacelet, J., Dohrmann, M., Díaz, M.-C., Cárdenas, P., Carballo, J.L., Ríos, P., Downey, R., & Morrow, C.C. 2020. World Porifera Database. Accessed at http://www.marinespecies.org/porifera on 2020-03-16. https//doi.org/10.14284/359

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The Triassic insects of Denmark Hill, Ipswich, Southeast Queensland: the creation, use and dispersal of a collection

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ABSTRACT

Type and additional fossil insects from the Late Triassic Denmark Hill locality in Southeast Queensland, Australia, are held in the collections of the Queensland Museum (Brisbane), the Australian Museum (Sydney) and the Natural History Museum of the United Kingdom (London). The history of these collections shows that they were the product of a concerted effort in the first two decades of the twentieth century to extract the fossils by Benjamin Dunstan, Queensland's Chief Government Geologist, and to describe the fossils by Dunstan and Robin Tillyard, the foremost Australian entomologist of the time. They collaborated closely to document the late Triassic insects of Australia, at the same time as Dunstan carefully curated and organised both the official government collection of these insects for the Geological Survey of Queensland, and his own private collection. The death of the two men in the 1930s led to the sale by his widow of Dunstan's private fossil collection (including type and type counterpart specimens) to the British Museum, and the donation of Tillyard's by his widow to the same institution, in addition to some material that went to the Australian Museum. This paper documents the locations of all of the published specimens. The history of the Denmark Hill fossils (a site no longer accessible for collection) highlights the problems for researchers of the dispersal of holdings such as these, and in particular the separation of the part and counterpart of the same insect fossils. It also raises ethical questions arising from the ownership and disposal of private holdings of important fossil material collected in an official capacity.

❑ *Mesozoic, palaeoentomology, Ipswich Coal Measures, Goodna, Duaringa, Tertiary.*

The Triassic insects of Denmark Hill in Ipswich, Southeast Queensland, were first discovered in the 1880s and described in a series of papers, mainly in the period 1916–1923. At that time they represented one of the most important Triassic insect faunas then known and because of their significance they attracted the attention of Robin Tillyard, a leading entomologist of that time.

In order to assist researchers studying this remarkable body of early fossil insects, this paper documents how the fossils were discovered, collected and curated, and then disposed of, and where the described specimens are now held.

This is also a story of three men – John Simmonds, an amateur naturalist, Benjamin Dunstan, Queensland's Chief Government Geologist, and Tillyard, who documented these fossils -- of the remarkable ten-year collaboration between Dunstan and Tillyard to bring these insects to the attention of science and the public, and of the vagaries of fate that led to their dispersal in the 1930s to three institutions in Australia and Great Britain.

The paper also highlights ethical questions relevant to public collections. The fossils had been collected primarily by Dunstan, they were in his care in his role as Queensland's Chief Government Geologist, but most of them

left Queensland as part of Dunstan's private collection. A small, but significant, private collection of John Simmonds also ended up as part of Dunstan's personal collection and was sold to the British Museum (Natural History).

RESEARCH APPROACH

This study arose because of the regular demand by researchers to access, at the Queensland Museum (QM) in Brisbane, a collection of Late Triassic fossil insects from Ipswich near Brisbane, first collected over 120 years ago. It was recognised that not all of the specimens were present at QM, nor was it clear where the other material might be located. The insects held at QM had been part of the original collections of the Geological Survey of Queensland (GSQ), which were amalgamated with the QM in 2003.

Research led the author to make enquiries of the Australian Museum (AM) in Sydney about their holdings of Denmark Hill fossils, the National Library of Australia (NLA) where Dunstan's papers had been copied and retained, and the National History Museum in London (NHMUK), its Archives and fossil insect registers. Papers relating to Dunstan and Tillyard were obtained from the NHMUK Archives and, once it was clear that the NHMUK had relevant fossil material, the staff at that museum kindly provided copies of the registers from the 1930s which clarified their current holdings of Dunstan specimens. GSQ Archives, held at the Queensland State Archives and the Queensland Museum, further filled out the historical picture of the fossil collections.

This is therefore a study based on documentary evidence, much of it previously not accessed, and is not an analysis of the fossils or the insects themselves. The published specimens are arranged taxonomically, using Jell (2004), and incorporating more recent taxonomic changes (see Tables 1 and 2). Reference is also made in Table 2 to some Tertiary specimens from Queensland and Triassic insects from Sydney, which were described at the same time by Tillyard, and of which some became part of Dunstan's private collection.

J.H. SIMMONDS, STONEMASON AND PLANT COLLECTOR

John Simmonds was born in 1862 and moved to Brisbane from Victoria in 1880 with his parents. Apprenticed to his father in the family stonemasonry business, which was successful and widely known, he eventually took over in 1889 (Dowe 2017). The Simmonds business may well have taken the younger Simmonds to Ipswich. By 1881 the firm was advertising its services widely, including in Toowoomba and Rockhampton (*Darling Downs Gazette*, 1 August 1881; *Rockhampton Morning Bulletin*, 20 July 1881) and by 1888 an 8-gallon water filter jar was being made by the Dinmore Brick and Tile Company (in Dinmore, rich in shales and clays and also a fossil plant locality, close to Ipswich) using a dripstone filter made by the Simmonds company, and embossed with the "John Simmonds" name (Ipswich Art Gallery 2004).

Being a stonemason by trade may have attracted Simmonds to studying rocks and collecting fossils in his spare time, but not necessarily to his other interests in botany and plant collecting. It was a combination of these interests that led him, an enthusiastic amateur naturalist, to make known the fossil plants and insects of Denmark Hill. As a founding member of the Royal Society of Queensland (RSQ) in 1884, he later became the secretary of its Field Naturalists section. Dowe (2017) documents Simmonds' collections and the botanical specimens which he collected and which are now held in a number of Australian and overseas herbaria.

Fossil plants were also a collecting passion of Simmonds, it seems. He first donated a "collection of fossil plants, Denmark Hill" to the Queensland Museum in July 1882 (QM Donations Register 1882-87: 11), and he was a significant donor to the Museum thereafter for the remainder of the decade. What prompted him to visit Denmark Hill is not known, although Frederick Whitehouse records that "early in the eighties of the last century the wealth of beautiful plant impressions, preserved in the typical blue and grey shales of the area,

were attracting attention" (*Queensland Times*, 17 September 1929). Simmonds was clearly one of the early collectors there. Prior to Simmonds arriving in Brisbane there had been a number of reports which highlighted the presence of fossil plants in the Ipswich region (especially in relation to the coal measures), notably Gregory (1876, 1879), Daintree (1872) and Carruthers in the same report, and Feistmantel (1880). Tenison-Woods (1882 and 1883) and Jack (1886) published more detailed surveys on Queensland fossils and geology, and Shirley (1898) used the Simmonds collection in his work on the fossil flora of Queensland, as did Walkom and Dunstan in 1915.

Denmark Hill, now located in the centre of the city of Ipswich, was then on the outskirts overlooking the growing commercial and industrial town. The hill became a popular location for large residences, the Ipswich hospital was built on its lower slopes in 1860 and a water reservoir was constructed as part of new water supply infrastructure in 1878. Contemporary images of Ipswich show Denmark Hill as far less wooded than it is today, and geological formations would have been clearly visible (as they are today in certain parts) as GSQ photos reveal (Tillyard & Dunstan 1916, Plate 9). Coal mining operations (the City Colliery, later named Noblevale No. 6) began mining the Aberdare seam under the hill from 1912 and in later years shafts were dug higher up and began to despoil some of the fossiliferous formations (Whitmore 1991). As a result, by 1936 the GSQ regretted that "the Denmark Hill beds at Ipswich are no longer available as a collecting ground" (Queensland Museum, Geological Survey of Queensland Archives: 003/36-0032). The original fossil beds remain inaccessible today, as they are part of a public recreation reserve, buried under spoil from the coal mine which closed in 1952.

Simmonds' fossil flora collection was widely regarded as "beautiful" and "magnificent" by Etheridge (Jack & Etheridge 1892: 347, 387; Walkom and Dunstan 1915: 1), and "of the very greatest value" (Shirley 1901: 42). As we know from his donations to the Queensland Museum, Simmonds had been collecting plants from Denmark Hill and other Ipswich localities since at least 1882, although it is possible he renewed his collecting efforts after the President of the RSQ suggested (perhaps somewhat belatedly) in August 1888 that Mr Simmonds "might, with advantage to himself and the Society, turn his attention to the fossil plants to be found in the Ipswich coal beds" (*Brisbane Courier*, 18 August 1888).

In his quest for fossil plants Simmonds also discovered fossil insects within the same plant bed, and the "Simmonds Collection" of insects was formed. It is unclear exactly when Simmonds collected his first insects from Denmark Hill, but they were first described in 1890 by Etheridge and Olliff, who referred to his "zealous researches" (Etheridge & Olliff 1890). His contact with Etheridge and Olliff probably came through fellow Royal Society member, R.L. Jack, Queensland Government Geologist, with whom Etheridge was collaborating on the major publication, The Geology and Palaeontology of Queensland and New Guinea (Jack & Etheridge 1892), and which sought to document the palaeontology of these areas. Jack records that Etheridge "examined the beautiful Collection of Plants made by Mr. J.H. Simmonds, of Brisbane, in August 1890" and identified insect and crustacean (conchostracan brachiopod) remains. Because of their similarity in age to the NSW Mesozoic strata, these fossils were included in Etheridge's 1890 publication with Olliff, on the New South Wales Mesozoic and Tertiary insects.

The "Simmonds Collection" of fossil insects from Denmark Hill consisted of seven items, two of which included part and counterpart. Etheridge and Olliff illustrated all of them, and described one species (*Mesostigmodera typica*), while Handlirsch several years later (1908) re-described it and also named four other beetles: *Ademosyne minor*, *Ademosyne major*, *Pseudorynchophora olliffi* and *Etheridgea australis*. Despite its only consisting of a few specimens, the Collection was nonetheless the starting point for the later extensive work by Dunstan, Tillyard and others on the Late Triassic insects of Ipswich.

BENJAMIN DUNSTAN, GEOLOGIST

Born in 1864, Dunstan was the son of a Cornish miner from a goldmining settlement near Castlemaine in Victoria. He graduated from Sydney Technical College in geology and became a lecturer there, and also worked as a consulting geologist. He was appointed as Assistant Geologist to the Geological Survey of Queensland in 1897. His passion for collecting was perhaps a natural result of his upbringing, and while in Sydney he collected widely from the Sydney Mesozoic sandstones at St Peter's, notably fossil fish, insects and a labyrinthodont (Tillyard & Dunstan 1916; NLA 1990: 1098). Dunstan was promoted to Acting Queensland Government Geologist in July 1902, being confirmed in the position in 1908. He served as head of the Queensland Geological Survey until his retirement in January 1931 (Sanker 1981; Denmead 1956).

Dunstan's achievements as head of the GSQ were significant, particularly the publication of the comprehensive Queensland Mineral Index and Guide (Dunstan 1913), and his encouragement of mapping (including aerial photography), coal exploration and palaeontological work. The Denmark Hill story owes much to his zeal. Denmead (1956) considered 1914 as the "heyday of Dunstan's rule".

In the Annual Reports of the Geological Survey, Denmark Hill is first mentioned by Dunstan in his Assistant Geologist's report in 1900, covering activities of 1899. He made many visits to Denmark Hill accompanied by an assistant, Mr W.T. Wilcox, to study and collect from the site. The early GSQ registers record Dunstan as the primary collector of the Survey's Denmark Hill plant specimens (but these entries would appear to have been made around 1912). Simmonds provided advice on the locations, and further insect-bearing strata were identified. Insects found were passed on to the Queensland Government Entomologist, Mr Tryon, for investigation and description (Queensland Department of Mines 1900: 194; Queensland State Archives, ID269545 Letterbook March 1899 to November 1900: 663-4; Tillyard & Dunstan 1916, 1923).

As there are no publications or reports, it seems that Tryon did not complete any substantial work on this material. He was, in any case, primarily engaged in economic entomology and plant pathology, including insect control of prickly pear (Anon. 1929). The first descriptions of the Denmark Hill insects by Tillyard and Dunstan were published in 1916.

According to Denmead (1956), Dunstan was "an expert mineralogist and had a passion for gemstones". Because he had been a lifelong collector of geological and fossil material, on his death in 1933 a large personal collection was left for his widow to deal with, a process of negotiation and sale that took until the 1950s to finalise through his daughter. It was Dunstan's keeping of a carefully curated personal collection (the "Dunstan Collection" or, as he referred to it, the "B. D. Collection"), that resulted in the dispersal of the Denmark Hill insect fossils and much other material obtained through his work and that of the Survey, and through his connection as head of the Survey.

At the same time, it is important to note that Dunstan's personal collection of the Denmark Hill insects was a by-product of his collecting in an official capacity on behalf of the GSQ – he was already employed by the Survey when he first went to Denmark Hill. Despite his government role, he retained a private collection of many hundreds of Denmark Hill specimens including types, "co-types" or type counterparts, which should perhaps have deposited with the GSQ. These included the Simmonds Collection of insects, as there exist no records of their transfer to him or to the Survey. This practice continued throughout his time at the Survey, including his period as Chief Government Geologist, when he made further "campaigns" (as he called them) to collect at Denmark Hill, adding to both the official and private collections. It was obviously the habit of an expert enthusiast, who perhaps felt that he had gone above and beyond his official duties, given the considerable effort he put in (as detailed below). His private collection also contained a wealth of other Queensland and NSW fossils, minerals and gemstones.

ROBIN TILLYARD, ENTOMOLOGIST

Tillyard was a significant figure in the history of entomology in Australia, arguably the leading authority in this country in the early decades of the twentieth century (Evans 1946; Imms 1936). Born in 1881, an Englishman by birth, Tillyard came to Australia in 1904 after gaining a Bachelor of Arts at Cambridge University. He taught at Sydney Grammar School before undertaking entomological research at Sydney University, being awarded his science degree in 1914, and later gained a lecturing position there. He had a particular interest in dragonflies, but it was in September 1913 that he first contacted Benjamin Dunstan at the suggestion of Professor Edgeworth David of Sydney University (himself a professional colleague of Dunstan) to ask whether he might work on the Ipswich fossil insects. Dunstan readily agreed, sent by post a first batch of specimens, and thus began a decade-long collaboration between the two men that led to the publication of 12 papers from 1916 to 1924 dealing with the Mesozoic insects of Queensland, primarily those from Denmark Hill.

Tillyard was chief of the Biological Department at the Cawthron Institute in Nelson, New Zealand from 1920–28, followed by six years as head of the Division of Economic Entomology at the Commonwealth Council for Scientific and Industrial Research in Canberra (CCSIR, later known as Commonwealth Scientific and Industrial Research Organisation, CSIRO). He achieved recognition for his work at both institutions on the role of insects in biological control, and published his major text, *The Insects of Australia and New Zealand,* in 1926 (Tillyard 1926). Tillyard's prolific palaeo-entomological work on Australian, American and British fossils continued, later investigating the newly-discovered deposits of Triassic insects at Mt Crosby, near Ipswich (Tillyard 1936; Tillyard 1937; Queensland Museum, GSQ Archives GSQ-003 1936).

Tillyard's health problems were a source of great trial to him and his family throughout his professional life, impacting on his work. He was injured in a railway accident at Milson's Point in Sydney, 1914, which affected him severely thereafter, suffering from many ailments over the years. He succumbed to a nervous breakdown in 1933 which led to early retirement from the CCSIR the following year (Ward 2013). He continued to research and publish after his retirement, but died as the result of a car accident in Goulburn NSW, on 13 January 1937.

Upon his death, his research collection had to be dealt with, a task which fell to his widow Patricia, liaising with both the British Museum and the Australian Museum. The dispersal of the Tillyard Collection is discussed below.

COLLECTING THE DENMARK HILL FOSSILS

The Denmark Hill site is part of the late Triassic Blackstone Formation (Purdy & Cranfield 2013), from the Late Triassic (Norian) period (-227—208.5Ma). The fossils occur in bands of shale with fossil plants and lie between the Aberdare and Bluff coal seams, just below the Aberdare seam and associated conglomerates. Now part of a local public reserve (-27.622° 152.756°), the fossil-bearing shales are today covered over and inaccessible, so further collecting is currently not possible.

Although we have no records of the collection of fossils by J.H. Simmonds, other than those listed from "within a small area on Denmark Hill" (Shirley 1898: iii), Dunstan provided detailed notes on the location, collection and curation of his Denmark Hill material (Tillyard & Dunstan 1916 and 1923; Tillyard 1917a).

Dunstan records that he visited the Denmark Hill site in 1899 with his assistant Wilcox, to reacquaint himself with the plant-bearing strata referred to by Shirley (1898). Dunstan noted that he located "a bed containing abundance of fossil flora, several species of insects, and numbers of a small crustacean, *Estheria mangaliensis*", now *Magniestheria mangaliensis* (Jones 1862) (Tillyard & Dunstan 1916; Queensland Department of Mines 1900: 194). In later paper Dunstan explained how he found another 6-inch layer containing

insects, a few feet higher up than the original "Simmonds shale" (Plan 1 and Map 2, Tillyard & Dunstan 1923, and Plates 8 and 9, Tillyard & Dunstan 1916).

> This fossil bed is of "finely arenaceous shale" and "the grain of the Ipswich shales and sandstone is fairly fine, so that the fossils, though sometimes rather faintly impressed upon the rock, offer the ideal conditions for study by strong oblique light. By this means the various sets of cross-veins in the wing venation can be brought into relief." (Tillyard & Dunstan 1916).

Dunstan clearly put a great deal of time and effort (official and private) into the collection, preparation and care of the fossil insects. While Simmonds had located the first few insect fossils from Denmark Hill, Dunstan devoted his energies to successive excavations over a number of years, and to the collection of a large amount of material that was subsequently curated and numbered, in addition to much material that was not. His personal passion for collecting no doubt drove him, but his senior position with the Geological Survey, and the fact that the Survey was at that time undertaking intensive work to map the Ipswich area for its coal measures, was perhaps an added incentive (Cameron 1899, 1907).

Undoubtedly, the effort involved in collecting the Denmark Hill insect material was considerable, both physically and in terms of the time taken to survey, map, extract and pack the split and unsplit shale blocks; transporting them from Ipswich to Brisbane by vehicle and rail, and then further splitting the rocks to study the fossils. The shales are located in steeply dipping strata, as vividly illustrated in Plate 9 in Tillyard & Dunstan (1916) and noted as dipping at 45° on Dunstan's map (Tillyard & Dunstan 1923). This required the removal of considerable overburden to access the fossiliferous strata. Mrs Ada Dunstan, in negotiating with the British Museum in 1935 over the purchase price of Dunstan's collection, spoke of "the 1000 little insect fossils on which my husband placed such high value. It has taken him years of finding and labour to get this fossil shale…" (NHMUK London, Museum Archives, *Dunstan*).

Dunstan himself described in early 1918 the frustrations of collecting as follows:

> Some days passed when the material was being split without a single specimen coming to light, and then one of these patches would be exposed, generally revealed by the finding of a fragment of a cockroach wing, which I consider the indicator insect, every care then being taken to split the shale into the thinnest possible plates. When this patch is exhausted, it might be days before another one is discovered. (Queensland State Archives ID269558 Letterbook January 1918-January 1919: 74)

It took some twenty years for Dunstan to gather the material, involving regular visits over that period. Tillyard indicated in 1916 that Dunstan's first collections were made "soon after he came to Queensland", which would coincide with Dunstan's reference to Denmark Hill in the Geological Survey Report for 1899. There was a further exploration in 1909, and Tillyard himself visited the site with Dunstan in late 1915 (NHMUK London, Museum Archives, *Tillyard*). More official fieldwork was undertaken after 1919, as a result of the international interest shown in the Tillyard publications (Queensland Department of Mines 1919: 154). Dunstan refers to his efforts in more detail in a letter to Tillyard on 20 February 1922:

> …I have been on a new fossil insect campaign…The material is now sorted out and we have got some startling results in the way of wings and tegmina…I have the boxes of material taken out to my house, and put in an hour every morning before breakfast and generally an hour in the evening….. We have about 75 boxes to split up and I reckon on getting an average of at least one good wing and one good tegmina in each, so there is about three years work ahead of us. (NLA 1990: 969-971)

In his paper on the fossil beetles (Tillyard & Dunstan 1923), Dunstan explains in detail his methods of extracting and preparing the fossils once the rock had been collected. He worked on the six-inch "fine clay shale" bed slightly above the original "Simmonds bed", exposing the quarry pavement by excavation and forming a "precipitous quarry face" (see Tillyard & Dunstan 1916 plate 9). After the overburden was removed, the bed was mapped and pegged, and Dunstan also prepared a careful plan of all the areas of shale extracted, which were then packed into separate boxes for examination, to determine if certain sections were richer in fossils. He had 100 boxes, each with 1½ square feet of the 6-inch shale in each box (NLA 1990: 149, 267-8 Ipswich Insect Quarry Plan). Dunstan recommended that more areas of the hill should be investigated, but it seems unlikely that that was done. The fineness of the sediments and plants within the shale would indicate a low-energy lentic environment, but Dunstan attributed the good preservation of insect material to the effect of Late Triassic hot springs causing a build-up of wings and tegmina from dead insects which were then buried, although there is no evidence to support this conjecture.

Dunstan also described in detail the laborious work of preparing the fossils from their shale matrix, and how the shale was split, the fossils found with hand lenses, and the fossil rock then trimmed and packed, with part and counterpart. He even suggested keeping the laboratory floor clean, so that fragments that fly off when splitting the rock could easily be found.

His recommended method of packing the fossil specimens was important for the future curation and identification of the "Dunstan collections". He proposed using "cardboard trays with covers, 1½ inches square and ¼ inch deep…sufficiently large for most of the specimens, the latter being cemented to the bottom of the tray with a liquid glue, or on to square pieces of cardboard fitting the trays…If the insects in the trays are packed away in boxes they should be numbered both on the cover and on the bottom of the trays… and if packed away on their ends, which is convenient, they should also be numbered on the top edges" (Tillyard & Dunstan 1923). The distinctive numbered small blue boxes of the Dunstan collection of insects, still extant today, are the result of Dunstan's careful curation of the original specimens.

FIG. 1. Dunstan's distinctive small blue boxes for the Denmark Hill fossils, with names and numbers handwritten by Dunstan

Dunstan records that "about 50 per cent of the [rock] material collected is discarded in the splitting and sorting, while the other 50 per cent, consisting of very small pieces showing no impressions on their surfaces, is repacked in the boxes for finer splitting at some future time" (Tillyard & Dunstan 1923). This detail is important, given that some 40 packing cases of Denmark Hill rock were purchased by Tillyard from Dunstan's widow after his death (see below) and are currently unaccounted for.

THE TILLYARD-DUNSTAN COLLABORATION

The analysis and description of the Ipswich insect fossils was a result of a decade of close

collaboration between Tillyard and Dunstan from 1913 until 1923. Dunstan, and his assistant Wilcox, were the primary field workers, and Dunstan held the specimens in Brisbane as "keeper" of the fossil site, particularly as he was head of the Queensland Geological Survey and the site was (as far as can be ascertained) on Crown land. Dunstan loaned the fossils in batches to Tillyard, who undertook the descriptions of most of the insect orders from his home in Sydney and later in Nelson, New Zealand. The Coleoptera, initially touched on by Tillyard in 1916, were described in full by Dunstan in 1923 (see below).

Of the series of 12 papers on the Mesozoic insects of Queensland, ten were written by Tillyard and published by the Linnean Society of New South Wales and two were produced jointly by Tillyard and Dunstan, published by GSQ. The first of these joint publications also included two Tertiary taxa from Queensland which were described as insects but of which one is a parastacid crustacean (Rozefelds 1985), and several Triassic insects from New South Wales, in addition to the Mesozoic Denmark Hill insects (see Tillyard 1917a, 1918–1923; Tillyard & Dunstan 1916, 1923).

Tillyard was dedicated to completing the work, despite ongoing ill-health and related setbacks, pressure of many other commitments as an entomologist (he was a world specialist on dragonflies, see Tillyard 1917b) and then as a senior scientist at the Cawthron Institute in New Zealand. His correspondence with Dunstan shows a level of formality on both sides, and it was not until much later that they occasionally addressed their letters as "Dear Dunstan/Dear Tillyard" rather than "Dear Mr Dunstan", although formality tended to prevail. Over the decade they visited each other several times in either Brisbane or Sydney, and frequently commiserated over each other's health problems.

Over the course of their collaboration, Dunstan would mail consignments of fossils to Tillyard in their "little blue boxes", who would then work on them. Tillyard then mailed specimens back to Dunstan when they had been described and published, although this could take a period of years. Tillyard's relocation to Nelson in New Zealand in 1920 further held up the work.

After the first report was completed (Tillyard & Dunstan 1916) Tillyard worked out a plan for the other papers. As Tillyard had a Fellowship from the Linnean Society of New South Wales there was a requirement that the papers were to be published by the Society. Throughout the long collaboration Tillyard expressed his thanks to Dunstan for the opportunity to work on the material, and for the latter's patience and forbearance. Tillyard referred frequently to the scientific value and importance of the Denmark Hill site, and the outstanding quality of the insects which he said were "beyond price to Entomology" (NLA 1990: 1023) and which could solve the outstanding problems of insect phylogeny, as he saw them at the time. The site "could have a finer show than Florissant" (NLA 1990: 1077), referring to the Eocene fossil deposits in Colorado, USA, which have produced a wealth of fossil insects. Tillyard even offered, on a couple of occasions, to put his own funds toward a more extensive excavation of the site, although Dunstan was reluctant to accept this offer. Tillyard was concerned that, after the publication of the 1916 paper, the site would become the target for "Yankees" eager to get hold of the insects for their collections. (NLA 1990: 1046 and 1048), and urged Dunstan to ensure that the site was protected.

The collaboration was, it would seem, a positive one, although there were tensions. Tillyard obviously found Dunstan hard to deal with, telling Bather of the British Museum in 1916 that "He is a peculiar fellow, and by no means an ideal man to have to work with" and complained of Dunstan's alterations to his figures (NHMUK London, Museum Archives, *Tillyard*). By late 1918 his opinion had not changed: "He is a most difficult person to get on with, and one never knows whether one is on his right side or his wrong side…You see how it is, I have to describe these insects from pure love of the job, not because of any thanks I get for doing it." (NHMUK London, Museum Archives, *Tillyard*)

For his part, Dunstan was frustrated with Tillyard and his lack of progress, although he appeared to understand Tillyard's physical and health limitations. Yet he telegraphed Tillyard in late 1917 to send a fossil wing immediately for reproduction, adding acerbically to the telegram "Might do better" (Queensland State Archives ID269557, Letterbook November 1916-January 1918: 706). There were arguments prior to the publication of the first paper published by GSQ. Dunstan complained in May 1916 to the Linnean Society of NSW (which had ordered reprints) about the quality of Tillyard's drawings, some of which (to Tillyard's annoyance) Dunstan had corrected, allegedly to avoid errors being published:

> …notwithstanding which I seemed to be blamed for daring to interfere in his work. If there is anything in this world Tillyard should be thankful for it is my severe criticism and revisal of this his first work before it appears in print. (Queensland State Archives ID269556, Letterbook 1915-1916: 546-8)

This criticism was made soon after a dispute occurred in regard to how the authorship of the first paper would be printed: not all the correspondence is available, but it would seem that the Queensland Government Printer had set the title page to give equal billing to both Tillyard and Dunstan. Tillyard reported to Dunstan that people in Sydney (possibly Robert Etheridge and William Dun from the Australian Museum) had said "that you evidently considered yourself as important as the author". Tillyard had argued that his own name be given primacy, and "I cannot help if I am open to a charge of little-mindedness…these little misunderstandings seem to be unavoidable at a distance…Let's try not to be suspicious of one another, and to remain as good friends as we were when I was in Brisbane" (NLA 1990: 1050).

Dunstan was privately angry at this, as revealed in his handwritten note on the back of the letter from Tillyard:

> Have drawn a lot of the figures, altered others, added to others, scribed them all on to the plates, altered and revised and edited his text, recast portions of it and put in a number of descriptions of new species, giving them the generic and specific names which Tillyard has adopted, and written a geological description of the three localities. All of this T. considers is simply an Introduction and therefore I should not consider myself "as important as the author", and should place my name second up onto a paper with his because I was not out for "KUDOS" as he expressed it.

These differences seem to have blown over, as the 1916 paper was jointly authored and collaboration continued, although the issue of who would describe the beetles (Coleoptera) from Ipswich remained unresolved. Tillyard expressed his dislike of working on beetles, as the elytra were difficult, if not impossible, to classify. In 1915 Tillyard suggested that Henry Tryon might be asked to undertake this task, but Dunstan pressed Tillyard to do it. Dunstan sent a consignment of beetles to Tillyard in mid-1918 and, after trying to get a fellow entomologist (H.J. Carter) to look at them, Tillyard began work on the illustrations, involving his wife ("who is splendid at wash-drawings") to paint them in half-tones – but Tillyard reiterated that "this work will take me a long time". (NLA 1990: 998) The job got put off until after the other insect orders had been dealt with, and eventually in February 1922 Dunstan proposed that he undertake the Coleoptera himself, leaving Tillyard to complete the remaining orders and a final summary paper – "otherwise it seems to me the work will be interminable" (NLA 1990: 970).

Tillyard welcomed this, and the paper on beetles was published in 1923 by the GSQ, not by the Linnean Society. The 1916 authorship disputes appear to have been forgotten, as the title page gave joint authorship to Tillyard and Dunstan (in that order), and referred to this paper as "Mesozoic Insects of Queensland Part 1: Introduction and Coleoptera", even

though it was the last one published. This was because Dunstan had arranged to bring all twelve papers together into a two-part volume, published by the Queensland Government Printer (Tillyard & Dunstan 1924).

DISPOSING OF THE DUNSTAN COLLECTION

Benjamin Dunstan died on 2 September 1933, after a "brief illness", believed to be cancer, and was buried at Toowong Cemetery in Brisbane. Probate on his estate was not granted until September 1937, due it would seem to the time taken to realise the value of his significant personal collection of fossils and minerals. This task was taken on by his widow, who endeavoured to sell this material to the British Museum. Dunstan's careful curation and documentation of the collection added to its significance.

Mrs Dunstan was prompted to contact the British Museum because her husband had previously sold them a skull and skeleton of a temnospondyl in 1927 (later described as *Paracyclotosaurus davidi* Watson 1958) for £500 (in 2020 value, about AUD$57,000), in addition to donating many fish specimens from his personal collection. Dunstan had collected the temnospondyl and fish from the St Peter's quarry in Sydney while working at the Sydney Technical College, and they were part of his personal collection.

Mrs Dunstan wrote to Dr Bather, Keeper of Palaeontology, on 18 June 1934 to seek their interest in the collection, which comprised fossil fish, insects, plants, trilobites, other ammonites, brachiopods etc., plus 100 pieces of the Queensland Tenham meteorite. A reply was received from Dr Lang, Bather's successor, Bather having retired and passed away in the interim. Lang initially offered £100, but once the material was packed and delivered to London, he agreed to pay £250 for the fossils, while the meteorite material was purchased separately for £100. Mrs Dunstan had appealed for a better valuation of especially the insects, "on which my husband placed such high value", but ultimately she accepted the amount offered (approximately AUD$32,000 in 2020 value) "as I feel sure you have conscientiously valued them" (NHMUK London, Museum Archives, *Dunstan*)

Mrs Dunstan approached the museum again in 1939 to see if they wanted to purchase more material, notably gemstones, fossil woods and lantern slides. Discussions were interrupted by the outbreak of war, but resumed soon after the war by Mrs Dunstan and her daughter Brenda. The gemstone collection was rejected, but Brenda Dunstan sent the lantern slides in 1955, which included a number relating to the fossil flora and fauna of Denmark Hill. Importantly, from an archival point of view, she also sent over Dunstan's notebooks, fossil registers, and the Dunstan-Tillyard correspondence, all of which are now digitally accessible (NLA 1990). The Museum was not interested in Dunstan's set of annotated geological maps, used in his work on the geology of Queensland, and their current whereabouts are unknown.

As a result, the British Museum holds a substantial collection of the insects from Denmark Hill, as the Dunstan arthropod specimens purchased in 1935 numbered 1112. We shall discuss below Dunstan's specimen lists and the current location of the various parts of his fossil insect collection.

DISPOSING OF THE TILLYARD COLLECTION

Tillyard had had to retire from government service in 1934 on medical grounds, although he still remained an active researcher, including an extended trip through Queensland in May and June 1936 (Lambkin 2020d). He died in January 1937, aged 56, but had a large number of fossil specimens on loan to him at that time, in addition to much material he had collected over the years. Among these were Denmark Hill fossil insects, Triassic insects from Mt Crosby in Queensland, and some 40 boxes of fossiliferous shale, thought to be from Denmark Hill, purchased by the Tillyards from Benjamin Dunstan's widow only a couple of years previously.

Tillyard's widow, Patricia, oversaw the disposal of this material. Patricia Tillyard was a graduate of Newnham College, Cambridge, graduating with Honours and a Masters from Cambridge in natural sciences (botany). She worked as a science teacher and collaborated with her husband over many years, including working as a scientific illustrator for the book, *Insects of Australia and New Zealand* (Tillyard 1926). As well as closely assisting her husband's work and nursing him through successive illnesses, Patricia was a well-known figure in Canberra society, as a hostess and head of the Girl Guides, Y.W.C.A. and other community, sporting and academic organisations. In short, Mrs Tillyard was used to dealing with institutions and authorities as her entry in the *Australian Dictionary of Biography* states: "She retained the supreme confidence of a 'Newnhamite' in her ability to chair a meeting, take charge of an organization, or entertain the highest in the land" (Clarke 1990).

Patricia Tillyard, who in June 1937 had travelled to England and her home town in Borstal, Kent for a 9-month period, entrusted the assessment and sorting of her husband's palaeontological collections to the Australian Museum in Sydney and her daughter Patience, who then worked in Canberra at the National Library. In general terms, Mrs Tillyard wanted most, if not all, the Tillyard collection to go to the British Museum, as a donation rather than a sale. Indeed, on arrival in England on 20 June, Mrs Tillyard was met by "officials of the British Museum", who took delivery of Tillyard's personal entomological collection of "500 Mayflies and 700 Dragonflies", including the types of 113 species. (*Canberra Times* 11 August 1937; *The West Australian* 22 June 1937)

Her stated motto in this instance was "when in doubt send to the British Museum", and there was extensive correspondence from July of 1937 until late 1938, when the Museum received the five packing cases of fossil specimens sent by the Australian Museum in Sydney on Mrs Tillyard's behalf (NHMUK London, Museum Archives, *Tillyard*). There was, for example, a considerable number of Triassic specimens from Brookvale in Sydney (insects, plants and fish including the important and spectacular orthopteroid *Clathrotitan andersoni* McKeown, 1937), the Permian of Newcastle, Permian Kansas insects, Cambrian trilobites from Mt Isa, and Cambrian archaeocyathinae from South Australia. There was also a separate consignment of 350 fossil insects from Mt Crosby near Ipswich in Queensland, which Dr Tillyard had collected on a trip to Queensland in May and June 1936. These now appear to reside at the NHMUK and have generated later research (Lukashevich & Shcherbakov 1999, citing NHMUK In.44958, R. J. Tillyard Colln.).

In fact, the Royal Society (London) had a direct interest in this last group of fossils because Tillyard, elected a Fellow of the Society in 1925, had received a Society grant in July 1935 in support of his post-retirement scientific activities. All material collected after that date, such as the Mt Crosby insects, belonged to the Society. They agreed, however, that these specimens should go to the British Museum with the "approval" of the Royal Society (NHMUK London, Museum Archives, *Tillyard*).

Other material that remained in Tillyard's possession after his death included Denmark Hill insects which Tillyard had been given by Dunstan in 1923, plus material which Tillyard had borrowed on a personal basis from the GSQ on 7 July 1936 (following his trip to Queensland), which he may have wanted as comparative specimens in assessing the Mt Crosby insects which he had just collected. The Australian Museum was keen to ensure that the material went back to their rightful owners, but the donated and borrowed Denmark Hill specimens (many of which were types and had been published) were retained at the Australian Museum, even those which had been borrowed from the GSQ. Two items did somehow find their way back to GSQ and are now in the QM. The whereabouts of the 40 boxes of Dunstan shale (referred to above) is unknown, although Mrs Tillyard was urged by the Museum in Sydney to forward the lot to London (NHMUK London, Museum Archives, *Correspondence Anderson*).

Interestingly, the GSQ was not an organisation to let missing specimens go astray, and on 24 September 1974 the Chief Government Geologist, Dr J.T. Woods, wrote to the Division of Entomology at the CSIRO Canberra, where Tillyard had worked prior to borrowing the fossils, enquiring if they had the specimens "in the little blue cardboard boxes in which they are still kept individually in our collection". The Assistant Curator of the Australian National Insect Collection confirmed there was no trace of the specimens in the collection but suggested some might be with the Australian Museum in Sydney and perhaps in "other hands". A "Personal" note sent on the same day to Woods said that one of the CSIRO curators, Dr Edgar Riek, had knowledge of the fossils but "refused to enlarge at all end" (Queensland Museum GSQ Archives: 013, 74/000126). This was disingenuous on Riek's part, as he had previously published on the Denmark Hill insects (Riek 1956), had used a number of the specific fossils about which the GSQ was enquiring, and his paper had referred to specimens in the Australian Museum, GSQ, the University of Queensland and the Dunstan Collection. These fossils have not been returned to the GSQ and still remain with the AM.

THE DUNSTAN REGISTERS

As noted above, Benjamin Dunstan was a meticulous administrator, and his attention to detail was demonstrated in the organisation of his personal collection of fossils and minerals. As discussed above, his approach to preparing and curating his insect fossils was precise, as was his cataloguing of the boxes of material extracted from Denmark Hill and the consequent "productivity" mapping of the Denmark Hill fossil field, where he indicated the most productive parts of the horizon (NLA 1990: 257-268). This search for completeness carried through to the tracking of the specimens he had loaned to Tillyard, and his proposed sorting of the identified and unidentified insects into several separate "categories".

This was demonstrated in his letter to Tillyard of 20 February 1922:

> I am sending you a list of fossils missing from our collections in duplicate, one of which I would like you to return showing specimens in your possession, the other you may retain. I would like returned what you actually do not require, but of course any that you may want in future will be forwarded to you at once. I am not forgetting the collection which you are to receive, but the longer this is left the more perfect it will be, as a great many duplicates exist, and the best of these are being sorted into three divisions – one for Department, one for you, and one for myself, the department collection of course being made as perfect as possible (NLA 1990: 969-73)

Dunstan eventually donated some fossils to Tillyard in 1923, 33 specimens in total, across 20 genera, not very many considering the many hundreds of insect specimens which Dunstan held.

The Dunstan registers of the Denmark Hill insects formed the basis for the eventual dispersion of the material, although it is not clear what prompted him to separate his material into the different groups, or to retain types or "co-types" in his personal collection. Whatever the reason, the result was that the department (GSQ) collection was certainly not as perfect as it should have been.

The Denmark Hill fossils he retained personally which are now held in the NHMUK were listed in his records as his "G", "D" and "S" Collections: "G" was the original Simmonds Collection of 7 specimens and two counterparts (although how and why these came into Dunstan's personal possession is not clear); "D" was the collection (numbered 1-367) that mirrored the official GSQ holdings, made up of parts or counterparts, including many types and type counterparts, plus some additional specimens; "S" was his Supplementary Collection (numbered 1-642, but including blank numbers) of additional uncited but identified specimens, plus some unidentified items. Also included was a separate group of 145 fragments,

some of which have since proved valuable: Kelly *et al.* (2018) described new dermapterans from two such fragments held at NHMUK.

LATER COLLECTIONS: EDGAR RIEK

There are no records of systematic collecting at Denmark Hill after Dunstan had completed his work, and by the mid-1930s the site was covered over by debris from the adjacent mine shaft. The entomologist Edgar Riek, however, reported in 1956 that both he and "staff of the Geology Department, University of Queensland", had made further collections at Denmark Hill, "from a slightly different horizon separated by three or four hundred yards from the original site…possibly not contemporaneous" (Riek 1956). This new location produced "beautifully preserved" insects, but Riek seems to have been deliberately vague in identifying the location in the UQ records and in the specimen labels, and the site has not been pinpointed in the intervening years. Riek did no further work there and the attention of University researchers shifted to study of the Late Triassic insects from Mt Crosby, some 10 km away.

University collection records have not revealed any further location data for the Riek material from Denmark Hill, although the UQ fossil collection (which was transferred to the QM in 1999) does hold Simmonds plant specimens from Denmark Hill, initially loaned to the Department of Geology's Museum for display purposes, and later donated by Simmonds, probably prior to 1942.

WHERE ARE THEY NOW?

The Denmark Hill insect fossils are now retained in three institutions: the Queensland Museum (Brisbane), the Australian Museum (Sydney) and the Natural History Museum (London). Types and type-counterparts are spread across the three locations, as set out in Table 1.

Queensland Museum, Brisbane (QM). The collection of Denmark Hill insect fossils held at QM (previously the GSQ Collection, transferred to QM in 2003) separately registers 344 Dunstan Denmark Hill specimens (including types and/or type counterparts). There are also 9 Denmark Hill specimens transferred with the UQ Collection in 1999. Five of the species described from Denmark Hill are not represented in the QM Collection.

Australian Museum, Sydney (AM). The AM collection consists of the Denmark Hill fossils held by Tillyard at his death in 1937. Some 30 items were borrowed by Tillyard from GSQ in July 1936, and others (as we noted above) had been donated to him from Dunstan in 1923 or (very few) loaned to Tillyard in 1923 but not returned. The AM therefore holds 64 Denmark Hill insect specimens in total, plus 8 other "Ipswich Qld" insects collected by Dunstan, probably from Denmark Hill. 23 of the published specimen numbers are currently held at the AM, including 10 of the type specimens.

Natural History Museum, London. The Denmark Hill insect specimens held in London are those sold to the British Museum (Natural History) (as it was then known) by Mrs Dunstan in 1935, as part of the Dunstan consignment. In total, there are over 1100 items, including 149 type, paratype, "co-type" or "type counterpart" specimens, which have been catalogued in the NHMUK fossil insect registers as part of the "Dunstan Collection". As noted, they are represent the "G", "D" and "S" groupings from Dunstan's personal collection.

It is worth noting that Dunstan did not lodge the historically important Simmonds Collection officially with the GSQ; but retained it with his personal holdings after retirement, and thus it also ended up with the NHMUK.

Table 1 lists all Denmark Hill specimens cited by Dunstan & Tillyard, and by Tillyard, plus additional Denmark Hill specimens cited by later researchers, and the uncited type counterparts held at NHMUK. Table 2 includes those fossils not from Denmark Hill described in Tillyard & Dunstan 1916 – important Sydney Triassic insects and the first fossil (an insect) described from Queensland's Tertiary Redbank Plains Formation -- and a

Cretaceous dragonfly from North Queensland (Tillyard 1918a). The table also lists the specimens of what was described in Tillyard and Dunstan 1916 as a Tertiary dragonfly from Central Queensland, which is now considered a parastacid crustacean (Rozefelds 1985).

The tables, organised by insect order, follow the arrangement set out in Jell (2004), except for the addition of Dermaptera in recognition of work by Kelly *et al.* (2018). Within each order, the described species are arranged alphabetically, as an easy finding aid. Unnamed but cited specimens are also included, as are *incertae sedis*. Original names later revised or synonymised are included with referral to the current name.

Information in the tables were drawn from the QM Vernon database, an Australian Museum list of their Dunstan material, and photocopies of the handwritten NHMUK registered entries from the "Dunstan Collection" material, accessioned between 1935 and 1937. These note the type and type-counterpart specimens, as indicated in Dunstan's original listing, provided to the NHMUK (NLA 1990: 696-714).

There are several minor anomalies referred to in the table notes. In particular, Table 2, two type counterpart specimens In.33592 and In.33593 at NHMUK are curiously listed in the register by the names originally proposed for the species, before being renamed and published (in Tillyard & Dunstan 1916) as, respectively, *Mesotitan giganteus* and *Notoblattites subcostalis*. The names were changed at the suggestion of Tillyard in a letter to Dunstan on 26 July 1915 (NLA 1990: 1088). The NHMUK register also incorrectly records the Goodna Tertiary insect (In.33309) as having been collected from Denmark Hill.

CONCLUDING COMMENTS

In writing this paper my aim was to bring attention to the whereabouts of the much-studied group of Denmark Hill fossil insects, and how they ended up in three separate institutions as a result of private holdings of official collections a century ago. These collections are internationally significant as they hold the type material of species from Australia, and under Australia's current Protection of Movable Cultural Heritage Act (1986) the sale and export of collections of this significance would not now be approved.

Splitting major collections has desirable and undesirable implications. Having this body of specimens in the northern hemisphere does provide access for researchers for whom London is a more convenient destination. At the same time, access is difficult for Australian researchers studying comparative material. Contemporaneous study of both part and counterpart of specimens may provide collectively more information than working from a single part, as details of fine venation and other features may not be adequately preserved in both. For most of the Denmark Hill taxa this side-by-side comparison is currently not possible. Furthermore, the NHMUK holdings are significantly greater in number than those in Australia, and include previously unstudied specimens which could be, and have been, used for re-assessment (e.g. Nel *et al.* 2002) and descriptions of new taxa (Kelly *et al.* 2018).

Sadly, Dunstan's aim cited above of creating an official GSQ collection "as perfect as possible" was not something he achieved, even though the material to do so was available to him. Instead, he chose to enhance his private collection, and while it is hard to assess Dunstan's decisions made over one hundred years ago, there are questions to ask. As a civil servant at the time he was diligent and competent, as his record as head of the GSQ shows, but it is not clear how he decided what was to be held in the government collection and what was able to be retained by him personally. Nor did he explain why he separated part and counterpart of most of the fossils, or why he chose personally to keep over three-quarters of all the numbered and prepared specimens.

In the ideal world, museums seek to digitise their holdings and make them accessible on-line, and it is important that in this way collections that have been split across different institutions can in time be digitally shared with all researchers who are interested in working on such material. Such a development would be of great benefit to those undertaking further study of the Denmark Hill fossil insect fauna, dispersed across nations as it has been for so long.

TABLE 1. Denmark Hill Fossil Insects: described species and location of specimens.
AM = Australian Museum (Sydney) Collection; BD = Benjamin Dunstan Collection GSQ = Geological Survey of Queensland Collection (now at Queensland Museum); NHMUK = United Kingdom Natural History Museum, London; QM = Queensland Museum, Brisbane; UQ = University of Queensland Geology Collection (now at Queensland Museum); Simmonds C. = Simmonds Collection.

Order and species name (as per Jell 2004), by collection locality	Where first described and published ("T&D" refers to "Tillyard & Dunstan")	Type number originally cited	Notes	Current location of cited specimen	Number at current location	Uncited type counterparts held at NHMUK	
						Original Dunstan number	NHMUK number
DENMARK HILL, QUEENSLAND							
Order ODONATA							
Mesomantidion queenslandicum	T&D 1916 T&D 1916	BD1a BD1b	Considered not an insect by Riek 1956	QM NHMUK	GSQ1a In.33278		
Mesophlebia antinodalis	T&D 1916; Tillyard 1922 Tillyard 1922	GSQ3a GSQ3b GSQ127a	Confirmed in Tierney *et al.* 2020	QM NHMUK AM	GSQ3a In.33279 AMF39270	BD127b	In.33397
Perissophlebia multiseriata	Tillyard 1918b Tillyard 1918b	GSQ203a GSQ203b		QM NHMUK	GSQ203a In.33467		
Triassagrion australiense	Tillyard 1922	GSQ290a		AM	AMF39253	BD290b	In.33544
Triassolestes epiphlebioides	Tillyard 1918b	GSQ205a	Counterpart discussed in Nel *et al.* 2002	AM	AMF39266	BD205b	In.33469
Triassophlebia stigmatica	Tillyard 1922	GSQ82a	Counterpart discussed in Nel *et al.* 2002	AM	AMF39267	BD82b	In.33352
Order PERLARIA							
Stenoperlidium triassicum	Riek 1956 Riek 1956 Riek 1956	UQC2244 UQC2245 AMF39256	Originally GSQ118	QM QM AM	UQC2244 UQC2245 AMF39256		
Order PROTORTHOPTERA							
Mesorthopteron locustoides	T&D 1916 T&D 1916 Tillyard 1922 Tillyard 1922 Tillyard 1922 Tillyard 1922 Tillyard 1922 Tillyard 1922 Tillyard 1922 Tillyard 1922 Riek 1956 Riek 1956	BD5a BD5b GSQ258b GSQ72a-b GSQ75 GSQ78a-b GSQ123 GSQ224 GSQ234 GSQ241b AMF39235 AMF39242	Originally GSQ53 Originally GSQ344a	NHMUK QM QM QM QM QM QM QM QM QM AM AM	In.33282 GSQ5b GSQ258b GSQ72a-b GSQ75 GSQ78a-b GSQ123 GSQ224 GSQ234a GSQ241b AMF39235 AMF39242	BD258a BD234b BD241a BD344b	In.33514 In.33496 In.33502 In.33583
Order BLATTARIA							
Austroblattula ipsviciensis	Tillyard 1919b Tillyard 1919b	GSQ105a GSQ105b		QM NHMUK	GSQ105a In.33375		
Austromylacrites latus	T&D 1916	BD8		QM	GSQ8		
Notoblattites? incertae sedis	Tillyard 1922 Tillyard 1922	GSQ100 GSQ162a		QM QM	GSQ100 GSQ162a		
Samaroblatta blabelloides	Tillyard 1919b	GSQ131b	Also referred to by Tillyard as "*blattelloides*"	QM	GSQ131b	BD131a	In.33401
Samaroblatta intercalata	Tillyard 1919b	GSQ262		QM	GSQ262		
Samaroblatta jonesi	Tillyard 1919b Tillyard 1919b	GSQ157a GSQ157b		QM NHMUK	GSQ157a In.33425		
Samaroblatta reticulata	Tillyard 1919b	GSQ155a		QM	GSQ155a	BD155b	In.33423
Samaroblatta triassica	Tillyard 1919b	GSQ156		QM	GSQ156		
Triassoblatta insignita	Tillyard 1919b	GSQ124		QM	GSQ124		
Triassoblatta intermedia	Tillyard 1919b	GSQ216		QM	GSQ216		

TABLE 1 cont…

Order and species name (as per Jell 2004), by collection locality	Where first described and published ("T&D" refers to "Tillyard & Dunstan")	Type number originally cited	Notes	Current location of cited specimen	Number at current location	Uncited type counterparts held at NHMUK	
						Original Dunstan number	NHMUK number
Triassoblatta typica	Tillyard 1919b Tillyard 1919b	GSQ180a GSQ180b		QM NHMUK	GSQ180a In.33444		
Blattoidea *incertae sedis*	Tillyard 1919b Tillyard 1919b Tillyard 1919b	152 121a 121b		QM QM QM	GSQ152 GSQ121a GSQ121b		
Order DERMAPTERA							
Phanerogramma australis *Phanerogramma dunstani*	Kelly *et al.* 2018 Kelly *et al.* 2018	In.35044 In.35041	Both are fragments from BD Collection	NHMUK NHMUK	In.35044 In.35041		
Order ORTHOPTERA							
Proparagryllacris crassifemur	Riek 1956 Riek 1956	AMF39251 UQC2134	Originally GSQ335a	AM QM	AMF39251 UQC2134	BD335b	In.33576
Triassolocusta leptoptera	Tillyard 1922	GSQ99		QM	GSQ99		
Triassomantis pygmaeus	Tillyard 1922	GSQ86a		QM	GSQ86a	BD86b	In.33356
Order PHASMATODEA							
Aeroplana mirabilis	Tillyard 1918b	GSQ126a	Placed in order Phasmodea by Riek 1956	QM	GSQ126a	BD126b	In.33396
Order HEMIPTERA							
Apheloscyta mesocampta	Tillyard 1922	GSQ98a		QM	GSQ98a	BD98b	In.33368
Chiliocycla scolopoides	Tillyard 1919c Tillyard 1922	GSQ158a GSQ327a		QM QM	GSQ158a GSQ327a	BD158b BD327b	In.33426 In.33571
Dunstania pulchra	T&D, 1916 T&D 1916	BD2a BD2b		QM NHMUK	GSQ2a In.33280		
Dunstaniopsis triassica	Tillyard 1918c Tillyard 1922	GSQ107a GSQ119a		QM QM	GSQ107a GSQ119a	BD107b BD119b	In.33377 In.33388
Eurymelidium australe	Tillyard 1919c	GSQ248a		QM	GSQ248a	BD248b	In.33509
Ipsvicia jonesi *Ipsvicia acutipennis* *Ipsvicia maculata*	Tillyard 1919c Tillyard 1923 Tillyard 1923 Tillyard 1923 Tillyard 1919c Tillyard 1919c Tillyard 1919c Tillyard 1919c	GSQ122a GSQ285a GSQ340a GSQ226 GSQ204a GSQ204b GSQ208a GSQ208b	Synonymised in Lambkin 2020c	QM QM QM QM QM QM QM NHMUK	GSQ122a GSQ285a GSQ340a GSQ226 GSQ204a GSQ204b GSQ208a In.33472	BD122b BD285b BD340b BD226b	In.33390 In.33540 In.33580 In.33488
Ipsviciopsis elegans *Ipsviciopsis magna*	Tillyard 1922 Tillyard 1922 Tillyard 1922	GSQ178a GSQ278a GSQ93a	Synonymised in Lambkin 2020c	QM QM QM	GSQ178a GSQ278a GSQ93a	BD178b BD278b BD93b	In.33445 In.33533 In.33363
Mesocixiodes orthoclada			See *Mesonirvana orthoclada*				
Mesocixiodes termioneura *Mesocixiodes brachyclada*	Tillyard 1922 Tillyard 1922 Tillyard 1922	GSQ88a GSQ325a GSQ4	Synonymised in Lambkin 2020b	QM QM QM	GSQ88a GSQ325a GSQ4	BD88b BD325b	In.33358 In.33569
Mesocixius triassicus	Tillyard 1919c	GSQ215		QM	GSQ215		
Mesodiphthera dunstani			See *Tardilly dunstani*				
Mesodiphthera grandis	Tillyard 1919c Tillyard 1919c Lambkin 2019	GSQ213a GSQ213b GSQ192a-b		QM NHMUK QM	GSQ213a In.33478 GSQ192a-b		
Mesodiphthera prosboloides			See *Tardilly prosboloides*				
Mesogereon affine	Tillyard 1921 Tillyard 1921 Tillyard 1921 Tillyard 1921	GSQ206a GSQ206b GSQ207a GSQ207b		QM NHMUK QM NHMUK	GSQ206a In.33470 GSQ207a In.33471		

TABLE 1. cont…

Order and species name (as per Jell 2004), by collection locality	Where first described and published ("T&D" refers to "Tillyard & Dunstan")	Type number originally cited	Notes	Current location of cited specimen	Number at current location	Uncited type counterparts held at NHMUK	
						Original Dunstan number	NHMUK number
Mesogereon compressum	Tillyard 1921 Tillyard 1921	GSQ144a GSQ144b		QM NHMUK	GSQ144a In.33413		
Mesogereon neuropunctatum	T&D 1916; Tillyard 1921	GSQ19a GSQ19b		QM NHMUK	GSQ19a In.33296		
Mesogereon shepherdi	Tillyard 1921	GSQ97		QM	GSQ97a	BD97b	In.33367
Mesogereon superbum	Tillyard 1921	GSQ169		QM	GSQ169a	BD169b	In.33435
Mesojassus ipsviciensis	T&D 1916; Tillyard 1919c Lambkin 2020a Lambkin 2020a Lambkin 2020a Lambkin 2020a Lambkin 2020a Lambkin 2020a	 GSQ33 GSQ56a-b GSQ90a-b GSQ111 GSQ220a-b GSQ240 GSQ265	Synonymised in Lambkin 2020a	 QM QM QM QM QM QM QM	 GSQ33 GSQ56a-b GSQ90a-b GSQ111 GSQ220a-b GSQ240 GSQ265	 BD111b 	 In.33381
Triassojassus proavitus	Tillyard 1919c Lambkin 2020a	GSQ191a GSQ282a		QM QM	GSQ191a GSQ282a	BD191b BD282b	In.33456 In.33537
Mesonirvana orthoclada	Tillyard 1922 Lambkin 2016a Lambkin 2016a Lambkin 2016a	GSQ318a GSQ91a-b GSQ193a GSQ324a-b	Revised in Lambkin 2016a as *Eoscartoides orthocladus* but replaced with *Mesonirvana* in Lambkin 2017	QM QM QM QM	GSQ318a GSQ91a-b GSQ193a GSQ324a-b	BD318b	In.33566
Mesoscytina australis *Mesoscytina affinis* *Triassoscarta subcostalis*	Tillyard 1919c Tillyard 1919c Tillyard 1919c Lambkin 2016b	GSQ112a GSQ235 GSQ116a GSQ320a-b	Synonymised in Lambkin 2016b	QM QM QM QM	GSQ112a GSQ235 GSQ116a GSQ320a-b	BD112b BD116b 	In.33382 In.33385
Paradunstania affinis	Tillyard 1918c	GSQ147		QM	GSQ147		
Tardilly prosboloides	Tillyard 1922; Lambkin 2019	GSQ89a	Revised in Lambkin 2019	QM	GSQ89b	BD89b	In.33359
Tardilly dunstani	Tillyard 1922 Lambkin 2019	no number GSQ317a	Revised in Lambkin 2019	QM	GSQ317a	BD317b	In.33565
Triassocixius australicus	Tillyard 1919c	GSQ267a		QM	GSQ267a	BD267b	In.33523
Triassojassus proavitus			See *Mesojassus ipsviciensis*				
Triassoscarta subcostalis			See *Mesoscytina australis*				
Unamed Homoptera	Tillyard 1919c	GSQ109a GSQ163 GSQ172a GSQ176a GSQ192a-b GSQ247a-b GSQ257a GSQ257b	In Dunstan's list, BD172 is listed as *Mesojassus ipsviciensis*	QM QM QM QM QM QM AM NHMUK	GSQ109a-b GSQ163 GSQ172a GSQ176a GSQ192a-b GSQ247a-b AMF39274 In.33515	BD172	In.33438
Order HETEROPTERA							
Triassocoris myersi	Tillyard 1922 Tillyard 1923 Tillyard 1922	GSQ140a GSQ150a-b GSQ167b		QM QM QM	GSQ140a GSQ150a-b GSQ167b	BD140b BD167a	In.33409 In.33434
Triassocoris scutulum	Tillyard 1922 Tillyard 1922 Tillyard 1923	GSQ134 GSQ184b GSQ179a-b		QM QM QM	GSQ134 GSQ184b GSQ179a-b	 BD184a 	 In.33450
Triassocoris ovalis	Tillyard 1923	GSQ129a		QM	GSQ129a	BD129b	In.33399

TABLE 1. cont…

Order and species name (as per Jell 2004), by collection locality	Where first described and published ("T&D" refers to "Tillyard & Dunstan")	Type number originally cited	Notes	Current location of cited specimen	Number at current location	Uncited type counterparts held at NHMUK	
						Original Dunstan number	NHMUK number
Triassocoris grandis	Tillyard 1923	GSQ196a		QM	GSQ196a	BD196b	In.33463
Order COLEOPTERA							
Ademosyne adunca	T&D 1923 T&D 1923	GSQ194b BD194a		QM NHMUK	GSQ194b In.33459		
Ademosyne australiensis	T&D 1916, 1923 T&D 1916, 1923 T&D 1916 T&D 1916 T&D 1916 T&D 1923	BD12a GSQ12b BD13 BD13b BD43 GSQ44		NHMUK QM QM NHMUK QM QM	In.33289 GSQ12b GSQ13 In.33290 GSQ43 GSQ44	BD43b	In.33317
Ademosyne brevis	T&D 1923 T&D 1923	GSQ339a BD339b		QM NHMUK	GSQ339a In.33579		
Ademosyne cameroni	T&D 1916, 1923 T&D 1916, 1923	GSQ46b BD46a		QM NHMUK	GSQ46b In.33319		
Ademosyne congener	T&D 1916, 1923 T&D 1916, 1923 T&D 1916, 1923 T&D 1916, 1923	GSQ40 BD41a GSQ41b GSQ42		QM NHMUK QM QM	GSQ40 In.33315 GSQ41b GSQ42		
Ademosyne curvata	T&D 1923 T&D 1923	GSQ274a BD274b		QM NHMUK	GSQ274a In.33529		
Ademosyne intermedia	T&D 1923 T&D 1923	GSQ233b BD233a		QM NHMUK	GSQ233b In.33495		
Ademosyne lata	T&D 1923 T&D 1923	GSQ132a BD132b		QM QM	GSQ132a GSQ132b		
Ademosyne major Handlirsch 1908	T&D 1916,1923 T&D 1916, 1923 T&D 1916, 1923 T&D 1916, 1923	S2 GSQ36a BD36b BD10	Simmonds Collection	NHMUK QM NHMUK NHMUK	In.33272 GSQ36a In.33311 In.33287		
Ademosyne minor Handlirsch 1908			See *Ademosynoides minor*				
Ademosyne olliffi	T&D 1916, 1923 T&D 1916, 1923 T&D 1923	S1 GSQ35 BD115	Simmonds Collection	NHMUK QM QM	In.33271 GSQ35 GSQ115a	BD115b	In.33384
Ademosyne parva	T&D 1923 T&D 1923	GSQ312a BD312b		QM NHMUK	GSQ312a In.33560		
Ademosyne punctata	T&D 1916, 1923 T&D 1916, 1923	GSQ47b BD47a		QM NHMUK	GSQ47b In.33320		
Ademosyne ramocostata	T&D 1923	GSQ225		QM	GSQ225		
Ademosyne rugulosa	T&D 1923 T&D 1923	GSQ260a BD260b		QM NHMUK	GSQ260a In.33516		
Ademosyne vittamargina	T&D 1923 T&D 1923 T&D 1923 T&D 1923	GSQ341a BD341b GSQ293a BD293b		QM NHMUK QM NHMUK	GSQ341a In.33581 GSQ293a In.33547		
Ademosynoides abnormis	T&D 1923 T&D 1923	GSQ243a BD243b		QM NHMUK	GSQ243a In.33505		
Ademosynoides alternata	T&D 1923 T&D 1923	GSQ149a BD149b		QM NHMUK	GSQ149a In.33418		
Ademosynoides angusta	T&D 1923 T&D 1923	BD15a GSQ15b		NHMUK QM	In.33292 GSQ15b		
Ademosynoides magnifica	T&D 1923 T&D 1923	GSQ199a GSQ199b		QM QM	GSQ199a GSQ199b		

TABLE 1. cont…

Order and species name (as per Jell 2004), by collection locality	Where first described and published ("T&D" refers to "Tillyard & Dunstan")	Type number originally cited	Notes	Current location of cited specimen	Number at current location	Uncited type counterparts held at NHMUK	
						Original Dunstan number	NHMUK number
Ademosynoides minor	T&D 1916, 1923 T&D 1916, 1923 T&D 1916, 1923 T&D 1916	S3 GSQ38b BD38a BD39	Simmonds Collection GSQ39 in QM Collection is *Samaroblatta reticulata*	NHMUK QM NHMUK NHMUK	In.33273 GSQ38b In.33313 In.33314		
Ademosynoides obtusa	T&D 1923 T&D 1923	BD9a GSQ9b		NHMUK QM	In.33286 GSQ9b		
Ademosynoides striatella	T&D 1923 T&D 1923	GSQ16a BD16b		QM NHMUK	GSQ16a In.33293		
Apheloodes obliquum	T&D 1923 T&D 1923	GSQ143a BD143b		QM NHMUK	GSQ143a In.33412		
Apheloodes rugosum	T&D 1923 T&D 1923	GSQ236a BD236b		QM NHMUK	GSQ236a In.33498		
Elaterites subulatus	T&D 1923 T&D 1923	GSQ263b BD263a		QM NHMUK	GSQ263b In.33520		
Elaterites transversus	T&D 1923 T&D 1923	GSQ159b BD159a		QM NHMUK	GSQ159b In.33427		
Elaterium bipunctatum	T&D 1923 T&D 1923	GSQ292a BD292b		QM NHMUK	GSQ292a In.33546		
Elaterium punctomarginum	T&D 1923 T&D 1923	GSQ200b BD200a		QM NHMUK	GSQ200b In.33464		
Etheridgea australis Handlirsch 1908	T&D 1916, 1923	S4	Simmonds Collection	NHMUK	In.33274		
Grammositum bilineatus	T&D 1923 T&D 1923	GSQ136a BD136b		QM NHMUK	GSQ136a In.33405		
Leioodes planum	T&D 1923 T&D 1923	GSQ348a BD348b		QM NHMUK	GSQ348a In.33585		
Leioodes pygmaeum	T&D 1923 T&D 1923	GSQ287a BD287b		QM NHMUK	GSQ287a In.33542		
Lobites granulatus	T&D 1923 T&D 1923	GSQ183b BD183a		QM NHMUK	GSQ183b In.33449		
Lobites trivittatus	T&D 1923 T&D 1923	GSQ164a BD164b		QM NHMUK	GSQ164a In.33431		
Lobites tuberculatus	T&D 1923 T&D 1923	GSQ342a GSQ342b		QM QM	GSQ342a GSQ342b		
Mesostigmodera typica Etheridge & Olliff 1890	T&D 1916, 1923 T&D 1916, 1923 T&D 1923 T&D 1923	S5a S5b GSQ61a GSQ61b	Simmonds Collection Simmonds Collection	NHMUK NHMUK QM QM	In.33275 In.33275 GSQ61a GSQ61b		
Mesothoris clathrata	T&D 1916, 1923 T&D 1916, 1923 T&D 1916	BD48a GSQ48b BD49		NHMUK QM NHMUK	In.33321 GSQ48b In.33322		
Mesothoris grandis	T&D 1923 T&D 1923	GSQ54a BD54b		QM NHMUK	GSQ54a In.33327		
Mesothoris quadripartita	T&D 1923 T&D 1923 T&D 1923	GSQ349a BD349b GSQ51a GSQ51b		QM NHMUK NHMUK QM	GSQ349a In.33586 In.33324 GSQ51b		
Mesothoris tenuiclathrata	T&D 1923 T&D 1923	GSQ313a BD313b		QM NHMUK	GSQ313a In.33561		
Platycrossos ligulatus	T&D 1923 T&D 1923 T&D 1923	GSQ268a GSQ268b BD118a-b	Listed as 118 at AM	QM QM AM	GSQ268a GSQ268b AMF39256	BD118a-b	In.33387

TABLE 1. cont…

Order and species name (as per Jell 2004), by collection locality	Where first described and published ("T&D" refers to "Tillyard & Dunstan")	Type number originally cited	Notes	Current location of cited specimen	Number at current location	Uncited type counterparts held at NHMUK	
						Original Dunstan number	NHMUK number
Platycrossos tumidus	T&D 1923 T&D 1923	BD45a GSQ45b		NHMUK QM	In.33318 GSQ45b		
Platycrossos subtumidus	T&D 1923	GSQ171		QM	GSQ171		
Polysitum minutus	T&D 1923 T&D 1923	GSQ336a GSQ336b		QM NHMUK	GSQ336a In.33577		
Polysitum punctatus	T&D 1923 T&D 1923	GSQ153b GSQ153a		QM QM	GSQ153b GSQ153a		
Pseudorynchophora olliffi Handlirsch 1908			See *Ademosyne olliffi*				
Reeveana intermedia	T&D 1923 T&D 1923	GSQ201b BD201a		QM NHMUK	GSQ201b In.33465		
Reeveana major	T&D 1923 T&D 1923	GSQ251a BD251b		QM NHMUK	GSQ251a In.33510		
Reeveana minor	T&D 1923 T&D 1923	GSQ297a BD297b		QM NHMUK	GSQ297a In.33550		
Shepherdia quadrivittata	T&D 1923 T&D 1923	GSQ130a BD130b		QM NHMUK	GSQ130a In.33400		
Simmondsia cylindrica	T&D 1923 T&D 1923	GSQ87a BD87b		QM NHMUK	GSQ87a In.33357		
Simmondsia subpyriformis	T&D 1923 T&D 1923	GSQ135 BD276	276 at QM is *Mesorthopteron*	QM NHMUK	GSQ135 In.33531	Paratype	In.32908
Tryoniopsis granulata	T&D 1923 T&D 1923	GSQ161a BD161b	Referred to as *Leptomorpha impunctata* in the BD list	QM NHMUK	GSQ161a In.33429		
Tryoniopsis punctata	T&D 1923 T&D 1923	GSQ250a BD250b	Referred to as *Leptomorpha granulata* in BD list	NHMUK QM	In.33511 GSQ250b		
Tillyardiopsis granulata	T&D 1923 T&D 1923	GSQ289a BD289b		QM NHMUK	GSQ289a In.33543		
Tillyardiopsis tuberculata	T&D 1923 T&D 1923	GSQ133a BD133b		QM NHMUK	GSQ133a In.33402		
Tillyardiopsis variotubercula	T&D 1923 T&D 1923	GSQ66a BD66b		QM NHMUK	GSQ66a In.33338		
Ulomites willcoxi	T&D 1916, 1923 T&D 1916, 1923	GSQ50b BD50a		QM NHMUK	GSQ50b In.33323		
Willcoxia magnopunctata	T&D 1923 T&D 1923	GSQ261a BD261b		QM NHMUK	GSQ261a In.33517		
Order NEUROPTERA							
Genus *Archeosmylus*	Riek 1956	AMF39249	Originally GSQ363	AM	AMF39249		
Archepsychops triassicus	Tillyard 1919a	GSQ137a	Became *triassicus* in Lambkin 2014a	QM	GSQ137a	BD137b	In.33406
Osmylopsychops spillerae	Tillyard 1923 Tillyard 1923	GSQ314a GSQ283a		QM QM	GSQ314a GSQ283a	BD314b BD283b	In.33562 In.33538
Petropsychops superbus	Riek 1956 Riek 1956	UQC2135 UQC2136	Became *superbus* in Lambkin 2014a	QM QM	UQC2135 UQC2136		
Protopsychopsis venosa	Tillyard 1917a	GSQ160a		QM	GSQ160a	BD160b	In.33428
Triassopsychops superbus	Tillyard 1922	GSQ284a	Became *superbus* in Lambkin 2014a	QM	GSQ284a	BD284b	In.33539
Order GLOSSELYTRODEA							
Polycytella triassica	Tillyard 1922 Tillyard 1922	GSQ81a GSQ154		QM QM	GSQ81a GSQ154a	BD81b	In.33351

TABLE 1. cont…

Order and species name (as per Jell 2004), by collection locality	Where first described and published ("T&D" refers to "Tillyard & Dunstan")	Type number originally cited	Notes	Current location of cited specimen	Number at current location	Uncited type counterparts held at NHMUK	
						Original Dunstan number	NHMUK number
Order MECOPTERA							
Archipanorpa magnifica	Tillyard 1917a Tillyard 1917a	GSQ106a GSQ120a	Proposed as *incertae sedis* in Riek 1956	QM QM	GSQ106a GSQ120a	BD106b BD120b	In.33376 In.33389
Aristopsyche superba			See *Mesopsyche triareolata*				
Mesochorista proavita	T&D 1916 T&D 1916 Riek 1956 Riek 1956	BD32a BD32b AMF39230 AMF39271	 Originally GSQ142a Originally GSQ142b	AM NHMUK AM AM	AMF39231 In.33308 AMF39230 AMF39271		
Mesopsyche triareolata *Triassopsyche dunstani* *Aristopsyche superba* *Neuropsyche elongata*	Tillyard 1917a Tillyard 1917a Tillyard 1919a Tillyard 1919a Riek 1956 Riek 1956	GSQ110 GSQ128a GSQ148a GSQ228a UQC2246 UQC2247	These 4 species synonymised in Riek 1956 and confirmed in Lambkin 2014b	AM AM AM AM QM QM	AMF39233 AMF39228 AMF39263 AMF39272 UQC2246 UQC2247	 BD128b BD148b BD228b	 In.33398 In.33417 In.33490
Neuropsyche elongata			See *Mesopsyche triareolata*				
Triassopsyche dunstani			See *Mesopsyche triareolata*				
Family Orthophlebiidae	Riek 1956	AMF39232	Previously GSQ52a	AM	AMF39232	BD52b	In.33325
Mecopteron *incertae sedis*	Tillyard 1919a	GSQ168a-b		QM	GSQ168a-b		
Panorpoid *incertae sedis*	Tillyard 1919a	GSQ114b	Also another 114A-B at AM as F39288 and F39286	AM	AMF39275 as 114a-b		
Order TRICHOPTERA							
Stereochorista frustrata	Tillyard 1919a	GSQ218	Reassigned from Mecoptera to Tricoptera in Riek 1956	QM	GSQ218		
Other specimens referred to							
Coleopterous larva burrow	Tillyard 1922	170	Possible leaf mine (Rozefelds & Sobbe 1987)	QM	GSQ170		
Insect fragment	T&D 1923 fig.61	350		QM	GSQ350		
Insect fragment	T&D 1923 fig.62	352		QM	GSQ352		
Insect fragment	T&D 1923 fig.63	353		AM	AMF39259	BD353	In.33587
Insect fragment	T&D 1923 fig.64	354		AM	AMF39261		
Insect fragment	T&D 1923 fig.66	355		QM	GSQ355		
Insect fragment	T&D 1923 fig.67	356		AM	AMF39258		
Insecta *incertae sedis*	T&D 1916 T&D 1916	6 7		QM QM	GSQ6 GSQ7		
Not *Mesorthopteron locustoides*	Tillyard 1922	GSQ5c		QM	GSQ5c		

TABLE 2. Other fossil insects from Tillyard & Dunstan 1916 and Tillyard 1918a: described species and location of specimens.

Order and species name (as per Jell 2004), by collection locality	Where first described and published ("T&D" refers to "Tillyard & Dunstan")	Type number originally cited	Notes	Current location of cited specimen	Number at current location	Uncited type counterparts held at NHMUK	
						Original Dunstan number	NHMUK number
ST PETER'S, SYDNEY							
Order BLATTARIA							
Notoblattites subcostalis	T&D 1916	BD25a	In.33593 is listed by NHMUK as the type counterpart of *Triassoblatta subcostalis*, the name originally proposed by Dunstan and Tillyard for this species	NHMUK	In.33593		
	T&D 1916	BD25b		QM	GSQ25b		
	T&D 1916	BD24a		NHMUK	In.33301		
	T&D 1916	BD24b		QM	GSQ24b		
Order TITANOPTERA							
Mesotitan giganteus	T&D 1916	22a		QM	GSQ22a		
	T&D 1916	22b	In.33592 is listed by NHMUK as the type counterpart of *Triassophlebia gigantea*, the name originally proposed by Dunstan and Tillyard for this species	NHMUK	In.33592		
	T&D 1916	21a		NHMUK	In.33299		
	T&D 1916	21b		QM	GSQ21b		
	T&D 1916	23a		NHMUK	In.33300		
	T&D 1916	23b		QM	GSQ23b		
Order COLEOPTERA							
Elaterites wianamattensis	T&D 1916	BD30		NHMUK	In.33306		
Etheridgea petrica	T&D 1916	BD31		NHMUK	In.33307		
Mesorhynchophora dunstani	T&D 1916	BD27a		NHMUK	In.33303		
		BD27b		QM	GSQ27b		
Metrorhynchites sydneiensis	T&D 1916	BD28a		QM	GSQ28a		
		BD28b		NHMUK	In.33304		
Insecta *incertae sedis*	T&D 1916	26a		QM	GSQ26a		
	T&D 1916	26b		QM	GSQ26b		
	T&D 1916	29a		QM	GSQ29a		
	T&D 1916	29b		QM	GSQ29b		
GOODNA, QUEENSLAND							
Order NEUROPTERA							
Euporismites balli	T&D 1916	GSQ34a		QM	GSQ34a		
	T&D 1916	GSQ34b	Incorrectly identified in NHMUK Register as "Upper Triassic, Denmark Hill". It is from the Tertiary Redbank Plains Formation in Southeast Queensland	NHMUK	In.33309		

TABLE 2. cont…

Order and species name (as per Jell 2004), by collection locality	Where first described and published ("T&D" refers to "Tillyard & Dunstan")	Type number originally cited	Notes	Current location of cited specimen	Number at current location	Uncited type counterparts held at NHMUK	
						Original Dunstan number	NHMUK number
DUARINGA, QUEENSLAND							
Order ODONATA (presumed)							
Austrolestidion duaringae	T&D 1916 T&D 1916	BD20a BD20b	Identified in Rozefelds 1985 as a parastacid crustacean, not a pair of zygopteran nymphs	QM NHMUK	GSQ20a In.33297		
ROLLING DOWNS, QUEENSLAND							
Order ODONATA							
Aeschnidiopsis flindersiensis Woodward	Tillyard 1918a	GSQ368		QM	GSQ368		In.64602

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LITERATURE CITED

ANON. 1929. Retirement of Mr Henry Tryon. *Queensland Agricultural Journal* **32**: 176-183

Cameron, W.E. 1899. On the Geology of the West Moreton or Ipswich Coalfield. *Geological Survey of Queensland Publication* **147**. Brisbane https://geoscience.data.qld.gov.au/

Cameron, W.E. 1907. Second Report on the West Moreton (Ipswich) Coalfield, with special reference to the Bundamba District. *Geological Survey of Queensland Publication* **204**. Brisbane https://geoscience.data.qld.gov.au/

Clarke, P. 1990. Tillyard, Pattie (1880-1971), *Australian Dictionary of Biography*. http://adb.anu.edu.au/biography/tillyard-pattie-8816

Daintree, R. 1872. Notes on the Geology of the Colony of Queensland. *Quarterly Journal of the Geological Society* **XXVIII**: 271-356. https://doi.org/10.1144/GSL.JGS.1872.028.01-02.40

Denmead, A.K. 1956, The Chiefs of the Geological Survey of Queensland from 1899 to 1955. *Proceedings of the Royal Society of Queensland* **LXVIII**: 51-60

Dowe, J.L. 2017. A family's contribution to Queensland botany: John Howard Simmonds [Snr] (1862–1955), Rose Simmonds (née Culpin) (1877–1960) and John Howard Simmons [Jnr] (1901– 1992). *Austrobaileya* 10 (1): 168–183. https://www.qld.gov.au/__data/assets/pdf_file/0026/69038/dowe-simmonds-austrobaileya-v10s1-p168-183.pdf

Dunstan B. 1913. Queensland Mineral Index and Guide. *Geological Survey of Queensland Publication* **241**. Brisbane. https://geoscience.data.qld.gov.au/

Etheridge, R. & Olliff, A.S. 1890. The Mesozoic and Tertiary Insects of New South Wales. *Memoirs of the Geological Survey of New South Wales. Palaeontology* **7**. C. Potter: Sydney.

Evans, J.W. 1946. Robin John Tillyard 1881-1937. *Proceedings of the Linnean Society of NSW* **71**, Memorial Series No. 11: 252-256

Feistmantel, O. 1880. Notes on the Fossil Flora of Eastern Australia and Tasmania. *Proceedings of the Royal Society of NSW* **XIV:** 103.

Gregory, A.C. 1876. *On the Coal Deposits of the West Moreton and Darling Downs Districts.* Brisbane, Legislative Assembly.

Gregory, A.C. 1879. *Geological Features of the South-Eastern Districts of the Colony of Queensland.* Brisbane, Legislative Assembly.

Handlirsch, A. 1908. *Die Fossilen Insekten und die Phylogenie der Rezenten Formen.* Leipzig.

Imms, A.D. 1936. Robin John Tillyard, 1881-1937. *Biographical Memoirs of Fellows of the Royal Society* **2**. https://doi.org/10.1098/rsbm.1938.0016

Ipswich Art Gallery 2004. *Ipswich Potteries 1873-1926.* Ipswich.

Jack, R.L. 1886. *Handbook of Queensland Geology.* Warwick and Sapsford: Brisbane.

Jack, R.L. & Etheridge, R. 1892. The Geology and Palaeontology of Queensland and New Guinea, with Sixty-eight Plates and a Geological Map of Queensland. *Geological Survey of Queensland Publication* **92**. Brisbane. https://geoscience.data.qld.gov.au/ https://doi.org/10.5962/bhl.title.131227

Jell, P.A. 2004. The Fossil Insects of Australia. *Memoirs of the Queensland Museum* **50**: 1-124.

Jell, P.A. (ed.) 2013. *Geology of Queensland.* Geological Survey of Queensland, Brisbane.

Kelly, R.S., Ross, A.J. & Jarzembowski, E.A. 2018. Earwigs (Dermaptera) from the Mesozoic of England and Australia, described from isolated tegmina, including the first species to be named from the Triassic. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **107**: 129-143 https://doi.org/10.1017/S1755691017000329

Lambkin, K.J. 2014a. Psychopsoid Neuroptera (Psychopsidae, Osmylopsychopidae) from the Queensland Triassic. *The Australian Entomologist* **41**(1): 57-76

Lambkin, K.J. 2014b. The Mesopsychidae (Mecoptera) of the Queensland Triassic. *The Australian Entomologist* **41**(3): 135-146

Lambkin, K.J. 2016a. Revision of the Dysmorphoptilidae (Hemiptera: Cicadomorpha: Prosboloidea) of the Queensland Triassic – Part 2. *Zootaxa* **4092**: 207-218 http://dx.doi.org/10.11646/zootaxa.4092.2.4

Lambkin, K.J. 2016b. Revision of the Scytinopteridae (Hemiptera: Cicadomorpha: Scytinopteroidea) of the Queensland Triassic. *Zootaxa* **4117**: 580-590 https://doi.org/10.11646/zootaxa.4117.4.9

Lambkin, K.J. 2017. *Mesonirvana* Evans, 1956, replaces *Eoscartoides* Evans, 1956 (Hemiptera: Cicadomorpha: Prosboloidea: Dysmorphoptilidae), a homonym of *Eoscartoides* Matsumura, 1940 (Hemiptera: Cercopidae). *Australian Entomologist* **44**(2): 61-62

Lambkin, K.J. 2019. *Mesodiphthera* Tillyard, 1919, from the Late Triassic of Queensland, the oldest cicada (Hemiptera: Cicadomorpha: Cicadoidea: Tettigarctidae). *Zootaxa* **4567**: 358-366 https://doi.org/10.11646/zootaxa.4567.2.8

Lambkin, K.J. 2020a. Revision of *Mesojassus* Tillyard, 1916, from the Late Triassic of Queensland (Hemiptera: Cicadomorpha: Membracoidea: Archijassidae). *Zootaxa* **4718**: 413-422 https//:doi.org/10.11646/zootaxa.4718.3.9

Lambkin, K.J. 2020b. Revision of the Hylicellidae of the Late Triassic of Queensland (Hemiptera: Cicadomorpha: Hylicelloidea). *Zootaxa* **4790**: 525-539 https://doi.org/10.11646/zootaxa.4790.3.7

Lambkin. K.J. 2020c. Revision of the Ipsviciidae of the Late Triassic of Queensland (Hemiptera: Cicadomorpha: Scytinopteroidea). *Zootaxa* **4860**: 503-520 https://doi.org/10.11646/zootaxa.4860.4.2

Lambkin, K.J. 2020d. Robin John Tillyard's 1936 Queensland excursion: uncivilized towns, unmitigated discomfort and fossil insects. *Archives of Natural History* **47**.1: 92-104 https://doi.org/10.3366/anh.2020.0624

Lukashevich, E.D. & Shcherbakov, D.E. 1998. A new Triassic family of Diptera from Australia. *Proceedings of the First International Palaeoentomological Conference,* Moscow. AMBA Projects AM/PFICM98/1.99: 81-89

National Library of Australia 1990. Australian Joint Copying Project, M2493. *Benjamin Dunstan (1864-1933) Papers 1913-1923.* Palaeontology Library, British Museum (Natural History) London https://nla.gov.au/nla.obj-838028448

Natural History Museum, London, Museum Archives, DF PAL/100/77. *Correspondence Anderson 1923-1939*

Natural History Museum, London, Museum Archives, DF PAL 100/112/9. *Dunstan, B. (Collection) 1914-1955.*

Natural History Museum, London, Museum Archives, DF PAL/100/212/28. *Tillyard, R.J. (1916-1938)*

Nel, A., Marie, V. & Schmeissner, S. *2002.* Revision of the Lower Mesozoic dragonfly family Triassolestidae Tillyard 1918 (Odonata: Epiproctophora). *Annales de Paléontologie* **88**: 189-214 https://doi.org/10.1016/S0753-3969(02)01049-2

Purdy D.J. & Cranfield, L.C. 2013. Ipswich Basin. Pp. 391-396. *In* Jell, P.A. (ed.) *Geology of Queensland.* Geological Survey of Queensland, Brisbane.

Queensland Department of Mines, *Annual Report 1900.* Brisbane https://geoscience.data.qld.gov.au/

Queensland Department of Mines, *Annual Report 1919.* Brisbane https://geoscience.data.qld.gov.au/

Queensland Museum. Queensland Museum Archives, *Donations Register 1882-1887*

Queensland Museum. Geological Survey of Queensland Archives, *Palaeontology files 1911-1935 and 1975-1977.*

Queensland State Archives, IDS7060 Series, *Geological Survey of Queensland Letterbooks 1877-1923.*

Riek, E. 1956. A re-examination of the mecopteroid and orthopteroid fossils (Insecta) from the Triassic beds at Denmark Hill, Queensland, with descriptions of further specimens. *Australian Journal of Zoology* **4**: 98-110. https://doi.org/10.1071/ZO9560098

Rozefelds, A. 1985. A fossil zygopteran nymph (Odonata) from the Late Triassic Aberdare Conglomerate, Southeast Queensland. *Proceedings of the Royal Society of Queensland* **96**: 25-32

Rozefelds, A. & Sobbe, I. 1987. Problematic insect leaf mines from the Upper Triassic Ipswich Coal Measures of southeastern Queensland, Australia. *Alcheringa* **11**: 51-57 https://doi-org.ezproxy.library.uq.edu.au/10.1080/03115518708618979

Sanker, I.G. 1981, Dunstan, Benjamin (1864-1933). *Australian Dictionary of Biography* **8** http://adb.anu.edu.au/biography/dunstan-benjamin-6056

Shirley, J. 1898. Additions to the fossil flora of Queensland, mainly from the Ipswich Formation Trias-Jura System. *Geological Survey of Queensland Publication* **128** *Bulletin* 7. Brisbane .https://geoscience.data.qld.gov.au/

Shirley, J. 1901. Australian vegetation and its geological development. *Proceedings of the Royal Society of Queensland* **16**: 39-44.

Tenison-Woods, J.E. 1882. On various deposits of fossil plants in Queensland. *Proceedings of the Linnean Society of NSW* **7**: 95-98. https://doi.org/10.5962/bhl.part.22733

Tenison-Woods, J.E. 1883. On the fossil flora of the coal deposits of Australia. *Proceedings of the Linnean Society of New South Wales* **8**: 37-167. https://doi.org/10.5962/bhl.part.28640

Tierney, A., Deregnaucourt, I., Anderson, J.M., Tierney, P., Wappler, T. & Bethoux, O. 2020. The Triassic Mesophlebiidae, a little closer to the crown of the Odonata (Insecta) than other 'triassolestids'. *Alcheringa* **44**: 278-285 https://doi-org.ezproxy.library.uq.edu.au/10.1080/03115518.2020.1730964

Tillyard, R.J. 1917a. Mesozoic Insects of Queensland. No. 1. Planipennia, Trichoptera, and the new Order Protomecoptera. *Proceedings of the Linnean Society of New South Wales* **42**: 175-200. https://doi.org/10.5962/bhl.part.4852

Tillyard, R.J. 1917b. *The Biology of Dragonflies (Odonata or Paraneuroptera).* Cambridge, Cambridge University Press. https://doi.org/10.5962/bhl.title.27401

Tillyard, R.J. 1918a. Mesozoic Insects of Queensland. No. 2. The Fossil Dragonfly *Aeschnidiopsis (Aeschna) flindersiensis* Woodward), from the Rolling Downs (Cretaceous) Series. *Proceedings of the Linnean Society of New South Wales* **42**: 676-692. https://doi.org/10.5962/bhl.part.4866

Tillyard, R.J. 1918b. Mesozoic Insects of Queensland. No. 3. Odonata and Protodonata. *Proceedings of the Linnean Society of New South Wales* **43**: 417-436.

Tillyard, R.J. 1918c. Mesozoic Insects of Queensland. No. 4. Hemiptera Heteroptera: the Family *Dunstaniidae*, with a Note on the Origin of the Heteroptera. *Proceedings of the Linnean Society of New South Wales* **43**: 568-592.

Tillyard, R.J. 1919a. Mesozoic Insects of Queensland. No. 5. Mecoptera, the new Order Paratrichoptera, and additions to Planipennia. *Proceedings of the Linnean Society of New South Wales* **44**: 194-212.

Tillyard, R.J. 1919b. Mesozoic Insects of Queensland. No. 6. Blattoidea. *Proceedings of the Linnean Society of New South Wales* **44**: 358-382.

Tillyard, R.J. 1919c. Mesozoic Insects of Queensland. No. 7. Hemiptera Homoptera; with a Note on the Phylogeny of the Suborder. *Proceedings of the Linnean Society of New South Wales* **44**: 857-896.

Tillyard, R.J. 1921. Mesozoic Insects of Queensland. No. 8. Hemiptera Homoptera (Contd.). The Genus Mesogereon; with a Discussion of its Relationship with the Jurassic Palaeontinidae. *Proceedings of the Linnean Society of New South Wales* **46**: 270-284. https://doi.org/10.5962/bhl.part.14018

Tillyard, R.J. 1922. Mesozoic Insects of Queensland. No. 9. Orthoptera, and Additions to the Protorthoptera, Odonata, Hemiptera and Planipennia. *Proceedings of the Linnean Society of New South Wales* **47**: 447-470.

Tillyard, R.J. 1923. Mesozoic Insects of Queensland. No. 10. Summary of the Upper Triassic Insect Fauna of Ipswich, Q. (With an Appendix describing new Hemiptera and Planipennia). *Proceedings of the Linnean Society of New South Wales* **48**: 481-498.

Tillyard, R.J. 1926. *The Insects of Australia and New Zealand.* Angus and Robertson. Sydney

Tillyard, R.J. 1936. New Upper Triassic Fossil Insect Bed in Queensland. *Nature* **138,** 719-720 https://doi.org/10.1038/138719b0

Tillyard, R.J, 1937. A Small Collection of Fossil Cockroach Remains from the Triassic Beds of Mount Crosby, Queensland. *Proceedings of the Royal Society of Queensland.* **XLVIII**, 5: 35-41

Tillyard, R.J. & Dunstan B. 1916. Mesozoic and Tertiary Insects of Queensland and New South Wales (with Six Text Figures and Nine Plates) Description of the Fossil Insects, also Stratigraphical Features by Dunstan B. *Geological Survey of Queensland Publication,* **253**. Brisbane. https://geoscience.data.qld.gov.au/ https://doi.org/10.5962/bhl.title.2497

Tillyard R.J. & Dunstan B. 1923. Mesozoic Insects of Queensland. Part 1 Introduction and Coleoptera by B. Dunstan. *Geological Survey of Queensland Publication* **273.** Brisbane https://geoscience.data.qld.gov.au/

Tillyard, R.J. & Dunstan, B. 1924, *Mesozoic Insects of Queensland, Parts I and II,* Brisbane, Department of Mines.

Walkom, A.B. & Dunstan, B. 1915. Mesozoic Floras of Queensland. Part. 1. The Flora of the Ipswich and Walloon Series. *Queensland Geological Survey Publication* **252**. Brisbane. https://geoscience.data.qld.gov.au/ https://doi.org/10.5962/bhl.title.7811

Ward, C. 2013. Robert John (Robin) Tillyard [1881-1937]. *CSIROpedia* https://csiropedia.csiro.au/Tillyard-Robert-John/

Whitmore, R.L. 1991. *Coal in Queensland: From Federation to the Twenties 1900 to 1925.* (University of Queensland Press: Brisbane)